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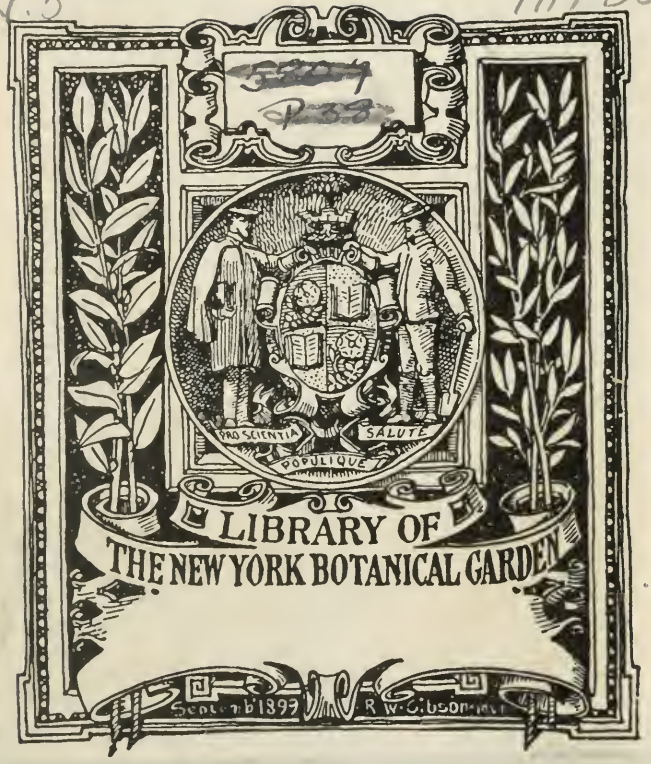

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UNIVERSITY OF PENNSYLVANIA
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The Macroscopic and Microscopic Structure of some Hybrid Sarracenias Compared with that of their Parents

By Alice Mary Russell, B.S., M.S.

[Thesis presented to the Faculty of the Graduate School in partial fulfillment of the Requirements for the Degree of Doctor of Philosophy.]

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Historical Review

Before Tournefort had named the genus *Sarracena* (1) and Linnaeus (2) had accepted the name, the group of the Sarracenias was already known to the early settlers in North America. They collected the plants and sent them to Europe as interesting exotics, where they were carefully described in botanical publications. As early as 1570, Lobel described specimens of the group which had come to his attention. Clusius (1601) (3) figures *S. purpurea* and Parkinson (4) copies his figure and adds a note which seems to indicate that he knew *S. flava* as well. Concerning this plant, which he calls "The Hollow Leaved Strange Plant of Clusius," he writes: "This strange plant hath such strange leaves, as the like are seldome seene in any other that we know growing, for they are nine or ten or more, rising from the head of a small long roote, each by itselfe, being small below, and growing greater upward, with a belly as it were bunching forth, and a bowing backe, hollow at the upper end, with a peece thereon like a flappe, and like unto the flower of *Aristolochia*, or Birthwort, and round at the mouth like a halfe circle, full of great darke purplish veins on the inside; the whole leaf is of thicke substance almost like unto leather; among these leaves sprang a stalke but was broken short off, so that what flower or seed it bore could not be observed. This was sent to Clusius from Paris by one that received it from Lishbone in the same manner. But of late Master John Tradescant the younger found this very plant in Virginia, having his toppe thereon, which he brought home and groweth with him, which I here show you with Clusius his figure. The leaves are longer, narrower and not bellying out, and the flower is borne at the top of the roundish seed vessell." The specimen sent by Tradescant was probably *S. flava*.

Plukenet (6) (7) was familiar with both *S. flava* and *S. purpurea*, since he gives very accurate figures of both species.

John Ray (8) gave a Latin translation of Parkinson's description already quoted. The actual specimen described by him, however, was a natural hybrid between *S. flava* and *S. purpurea*, and was the first natural hybrid collected. (See below.)

Tournefort named the genus *Sarracena*, in honor of Dr. Sarrasin of Quebec (1), and described one species, *S. canadensis*. Linnaeus accepted the genus name and described the two species long recognized, *S. flava* and *S. purpurea*.

Walter, in 1788 (9), described and named two new species, *S. minor* and *S. rubra*. *S. psittacina* was added to the genus by Michaux in 1803 (11). Croom (12) described *S. Drummondii* in 1835.

Since the above time, only one new species has been added, *S. Sledgei* in 1906, by Macfarlane (17).

A few of the botanical publications of this time review the genus as varying in composition:

"Flore des Serres" (13) gives seven species: *S. flava* (L.), *S. purpurea* (L.), *S. variolaris* (= *minor* Walt. = *adunca* Smith), *S. undulata* (Dcn.), *S. Drummondii* (Cro.), *S. rubra* (Walt.), *S. psittacina* (Michx.) (= *calceolata* = *pulchella* (Croom)). Chapman (14) gives all of the above except *S. undulata*, which he considers synonymous with *S. Drummondii*. Hooker (15) mentions eight species but does not enumerate them. Boulger (16), in reviewing the genus, has the six species: *S. purpurea*, *S. flava*, *S. rubra*, *S. Drummondii*, *S. psittacina*, *S. variolaris*.

During the latter half of the 18th century, Sarracenias were widely cultivated in European gardens. New varieties were eagerly sought for exhibition, many new forms were introduced from America and several artificial hybrids were produced. Since each exhibitor appended a name to his own product, a great confusion of names had arisen and a survey of the forms under cultivation became most necessary. Dr. Masters, therefore, undertook the review in three numbers of the Gardeners' Chronicle for the year 1881 (18). Here he gives a key to the forms raised in English gardens and gives for each a short description from living specimens furnished to him. The forms and species described by him are as follows:

1. *S. psittacina* (Michx.) A. D. C. Prod. XVII, p. 4.
2. *S. purpurea* (L.) A. D. C. Prod. XVII, p. 4.
3. *S. Chelsoni* × (Hort. Veitch, G. C. vol. 9, p. 11 (*rubra* × *purpurea*).
4. *S. variolaris* (Michx.) Croom. A. D. C. Prod. XVII, p. 6.
5. *S. Drummondii* (Croom) A. D. C. Prod. XVII, p. 5 (var. *alba* G. C. vol. 10, p. 281).
6. *S. undulata* (Dcn.) = *S. Drummondii* (Croom) Rev. Hort. i, p. 126. Flore des Serres 7, A. D. C. Prod. XVII, p. 5. Index Amer. Bot. p. 40.

7. *S. rubra* (Walt.) Flora Car. p. 152. (Croom) A. D. C. Prod. XVII, p. 4. var. *acuminata* (A. D. C. loc. sit.) var. *Sweetii* (A. D. C.) Wat. Index p. 40 = *S. minor* (Sweet) = *S. rubra* (Planchon).
8. *S. flava* (L.) Sp. Pl. Ed. i, p. 510. A. D. C. Prod. XVII, p. 5. var. *Catesbaei* (Ell.) Bot. S. Car. = *S. flava* var. *picta* Hort. Bull. = *S. Fildesii* Hort. Williams.
   Var. *ornata* (Hort. Bull.).
   Var. *Rugelii* (Shuttleworth) = *erythropus* Hort. Bull., A. D. C. Prod. XVI, p. 6.
   Var. *limbata* (Hort Bull.).
   Var. *maxima* (Hort. Angl.).
   Var. *cristata* (Hort. Bull.).
   Var. *atrosanguinea* (Hort. Bull.).
   Var. *minima* (Hort. Angl.).
9. *S. Moorei* × (G. C. 1874, p. 702 = *S. Drummondii* × *S. flava*).
10. *S. Stevensii* × (G. C. 1874, p. 738) = *S. flava* × *S. purpurea*).
11. *S. Williamsii* × (Hort. Williams above 10).
12. *S. Popei* × (*S. flava* × *S. rubra*).
13. *S. melanorhoda* × (Hort. Veitch. *S. purpurea* × *S. Stevensii*).
14. *S. formosa* × (Hort. Veitch. *S. psittacina* × *S. variolaris*).

The above review constitutes the basis for the article on Sarracenias in Nicholson's Dictionary of Gardening (20).

The history of the hybrids grown during this period is interesting. In 1874 the first artificial hybrid was produced and exhibited by Dr. Moore at the International Botanical Congress in Florence. An abstract of Dr. Moore's paper upon the presentation of the hybrid is given in the Gardeners' Chronicle 1874, p. 738. Of the plant, which had *S. flava* as the female and *S. Drummondii* as the male parent, he writes: "The plant is as nearly as possible intermediate between those two noble species of the genus, and no hybrid which has hitherto come under my notice proves more decidedly than it does the marked influence of the pollen of one plant applied to the stigma of another. . . . During the months of April and May most of the species flower and produce young leaves, after perfecting which the plants rest six weeks or more, when some of the kinds produce a second crop of leaves which remain fresh during the winter and are more beautiful than those of the first crop. This is especially the case with *S. Drummondii*. . . . *S. flava* does not make a second growth of leaves in so marked a manner, but rather inclines to rest during the winter months." "Now it is in the mixture of the leaves that the intermediate state of the hybrid is so strikingly exemplified. It makes a second

growth of winter pitchers similar to *S. Drummondii*, and these are nearly as highly colored, but they decay much sooner than those of the parent species and thus resemble more those of the female parent, *S. flava*. Further, the large stature of the plant, nearly two feet high, the purple color of the flowers, and, indeed, everything connected with it, shows that it holds an exactly intermediate rank between the parents." Shortly afterwards Messrs. Veitch and Sons were awarded a prize for a hybrid between *S. flava* (female) and *S. purpurea* (male), and named in honor of the gardener whose product it was, *S. Stevensii*. A hybrid of the same parentage, but of natural origin, was exhibited under the name *S. Williamsii*, in honor of the man who discovered it among a mass of *S. flava* shipped to him from the Southern States (22). Other artificial hybrids were shortly afterwards exhibited and are noted above by Masters.

The most recent review of the genus is that of Macfarlane in "Pflanzenreich" (23). All of the species and hybrids noted above are given, but a new species is here added, *S. Sledgei* (17). Macfarlane reviewed and fully described the supposed species *S. Catesbaei* (24) in order to eliminate the confusion which had arisen through ascribing to it forms such as *S. rubra*, *S. flava*, etc., because of Elliot's meager description, and the misplacing of his type specimen. The plants used as type specimens by Macfarlane were first obtained through Dr. Sledge, of Mobile, who sent them north, where they were grown in the Sarracenia House at the University of Pennsylvania Botanical Garden. The pitchers and flowers were typical, Macfarlane found, of plants cultivated abroad under the names *S. flava*, var. *cristata*, *S. flava*, var. *picta*, or *S. flava*, var. *Catesbaei*. A visit to the region established the fact that these plants grew in pure stands and were indigenous to the locality, so they were used as type forms on which the description of the supposed species *S. Catesbaei* was based. Later the type of Elliot for the above species was found in the Charleston Museum, and proved to be a specimen of the natural hybrid between *S. flava* and *S. purpurea*. A new name was therefore applied to the genus described by Macfarlane, *S. Sledgei*. In regard to the new species he writes: "So far as accurate records show, *S. Sledgei* seems to be confined to the Gulf region between the Alabama River and Eastern Texas, over which area it may at times be extremely abundant.

It is here only associated with *S. psittacina* and *S. purpurea*, both of which flower from one to two weeks later. In spite of this there is every likelihood that hybrids will in time be reported, for the flowers of all species last for 14 to 21 days" (17).

Since the time this was written, the author himself has found *S. Drummondii* growing with *S. Sledgei*, and with them quantities of the cross which he has named *S. areolata*. Macfarlane (26) gives the following note concerning this plant:

"It is a frequent hybrid wherever both parents are present near each other. It is especially abundant near Mobile, Ala., and westward for thirty miles."

Natural Distribution of Species and Hybrids Selected for Study

Of the forms to be studied, *S. purpurea* is the best known and most widely distributed (23). It is found from Labrador through Newfoundland, Quebec, Manitoba, Michigan, Wisconsin, and from thence southward to Indiana. Along the coast it extends from New England to Florida in the swampy regions back as far as the Alleghany Mountains. In the south it is plentiful about the Gulf region from Florida to Louisiana.

S. flava has a more restricted distribution (23). It is more or less abundant from southern Virginia, through North and South Carolina, Georgia, Florida, and eastern Alabama.

Therefore, the hybrid between these species might be found in the region from North Carolina to eastern Alabama. It is reported from Wilmington, N. C., and Ponce de Leon, Florida. Possibly additional localities may be reported from Georgia (23) and South Carolina.

S. Drummondii is found only between south central Georgia and western Alabama (23). Since *S. flava* is never found west of the Alabama River, the hybrid would not be expected outside of southern Georgia, Florida, and eastern Alabama. Specimens have been gathered in Georgia (Americus), in Florida (Milligan and Crestview), and from Alabama (Bay Minette and Deer Park).

S. Sledgei, most recently described species, is limited to the region about the Gulf, west of the Alabama River (23). There are specimens preserved from Alabama, Louisiana, and east-

ern Texas. Additional localities may yet be reported. The hybrid, *S. areolata*, with *S. Drummondii*, is therefore to be sought only between Alabama River and western Alabama. It is especially plentiful at two points, Theodore, Alabama, where it was first found, and Deer Park.

The above are the species and hybrids selected for study. The material used was from natural sources indicated above, transplanted to the University of Pennsylvania Botanical Garden.

It might be well to note here the other natural hybrids reported by various collectors. Besides the above three, there are given (23; 17):

S. flava × *S. minor.*
S. minor × *S. psittacina* (grown in University of Pennsylvania).
S. rubra × *S. Drummondii.*
S. psittacina × *S. purpurea.*
S. rubra × *S. purpurea* (grown in University of Pennsylvania).
S. Drummondii × *S. purpurea* (grown in University of Pennsylvania).
S. Sledgei × *S. purpurea* (grown in University of Pennsylvania).

The study was limited to three groups, with one parent common to two hybrids in order the better to ascertain the action of a given parental characteristic.

Comparison of Parents and Hybrids

Set 1. S. purpurea, S. flava, and S. Catesbaei (S. Stevensii)

A. Naked Eye Characters

The general habit of *S. purpurea* is shown well in Pl. I, fig. 1, with its inflated pitchers, and the decumbent leaves. *S. flava* presents a striking contrast to *S. purpurea* (Pl. I, fig. 2). The pitchers are erect, slender, and gradually expanded upwards. In the hybrid (Pl. I, fig. 3) the pitchers lean at an angle of 45°, and are slightly inflated in their middle portion.

In height the three forms present a wide range. *S. purpurea*, the lowest, averages 12–15 cm., though specimens can be found 35 cm. in length. *S. flava* may be from 20–100 cm. high, but average pitchers measure 60–70 cm. from base to the tip of the lid. The hybrid averages 24–36 cm. in length.

The "wing," or fused laminar faces in front of the pitcher proper, is wide in *S. purpurea* (Pl. I, fig. 1) and tends to have an undulating margin. In *S. flava* the wing is very narrow

(Pl. I, fig. 2) and extends the whole pitcher length. In *S. Catesbaei* the wing is wider below, half as wide as in *S. purpurea*, and of much the same shape (Pl. I, fig. 3).

In *S. purpurea* the inflated pitcher is constricted below the rim around the mouth (Pl. I, fig. 1). In *S. flava* the pitcher has no suggestion of a constriction, but rather expands widely at the rim. In *S. Catesbaei* the pitcher is slightly constricted below the rim (Pl. I, fig. 1), although not so strongly as in *S. purpurea*.

The color of the pitchers of *S. purpurea* is: base green with a reddish network of veins over the outer pitcher surface, particularly above. The lid is especially strongly marked with crimson-purple reticulations. (Variations: all green; with graded transitions to crimson-purple suffused over the surface almost uniformly.) *S. flava*, in the most common type, has a greenish yellow pitcher and lid, the latter with a deep crimson patch at its base. The marking is usually band shaped, about 1–2.5 cm. wide. (Variations: purplish veining on upper pitcher and lid; bright green pitcher; or entire pitcher and lid rich purple.) *S. Catesbaei* shows a variety in coloration, according to the variations noted above in the parents. An average type represented in fig. 3 has a green pitcher with red-purple veinings, less heavily developed than in *S. purpurea*. The red banding in the throat of the *S. flava* parent is reproduced, but more dilute in color. (Variations: uniformly green, more pronounced purple markings, or entirely purplish.)

The lid shape in the three forms exhibits a nearly balanced relation. In *S. purpurea* the lid is reniform, with an undulate margin (Pl. I, fig. 1). The lower lateral portions of the lid are prolonged into blunt lobes, which are bent forward about the mouth of the pitcher, so that it is open only from the front. Instead of overhanging the pitcher opening, the lid in this species is somewhat curved outwards. In *S. flava*, the lid is ovate-cordate, but prolonged in its median portion into a tip process. The sides of the lid are not lobed as deeply as in *S. purpurea*, but the slight auricles are here bent sharply backwards, exposing the throat of the pitcher. The lid slightly incurves above the orifice. *S. Catesbaei* (fig. 3) is very nearly intermediate in parental characteristics. The lid is more rounded in outline than *S. flava*, but possesses a slight tip process, not as pro-

nounced as in *S. flava*. The lobes are intermediate in size, in position also, since they stand straight out from the side of the pitcher. The margin of the lid is wavy, with looser undulations than in *S. purpurea*. The lid does not overhang the pitcher mouth, but is erect.

B. Microscopic Study of the Pitchers

I. Methods.

Three methods were used in preparing the epidermal surfaces described below.

(*a*) Scrapings of fresh material were made, for comparison with treated material to gauge possible shrinkage, or seeming abnormalities.

(*b*) Scrapings of material macerated in KOH.

(*c*) Strips of pitcher parts were boiled in 25%–50% HNO_3, to which a pinch of $KClO_3$ was added. When the material appeared white, or bleached, it was quickly placed in water. The mesophyl and subepidermal cells could be easily brushed off and both upper and lower epidermis could be mounted in acetic acid side by side for comparison; sealed with asphaltum. The nitric acid was not used in such strength that cell walls were affected. The delicate hair striations appear clearly in the photographs (Pl. IV, figs. 15 and 16) made from such slides with the aid of the Edinger apparatus.

Ordinary paraffin material, fixed in chrom-osmo-acetic or weak chrom-acetic, was used for sections mentioned.

In counts given for a "field," it will be understood, unless distinctly stated otherwise, that the standard "field" is that of a No. 3 Bausch and Lomb eyepiece, and a No. 4 mm. Bausch and Lomb objective.

Averages are based on 100 or more counts, and measurements on 200 or more. Corresponding portions of corresponding surfaces were carefully selected for comparison.

Outer Epidermis of the Lid

In all three forms, the outer epidermis of the lid shows cells that are roughly quadrangular, with wavy walls. Normal stomata are present, and simple unicellular hairs. In general these hairs point upwards toward the edge of the lid. Glands, similar to those of the interior pitcher area, are scattered over this outer surface somewhat irregularly.

In *S. flava* the epidermal cells are longer than broad (Pl. III, fig. 9) with an angular wavy wall. Stomata are fairly numerous, seven to a field, and of the same size as within the pitcher (.035×.030 mm.). Glands are less numerous than within on the specially modified surfaces, one only to a field averagely. The unicellular hairs mentioned above are in *S. flava* blunt, with a decided bending or hooking in some, while in others the axis is straight or merely slightly curved. They vary greatly in size, from mere knobs .01 mm. long to .1, .2, .3 mm. in length. Pl. III, fig. 9 will show the range of size and shape in these hairs. It will be noted that in all the surface of the hair is raised in wart-like thickenings, which at times lie in lines parallel to the axis of the hair, and suggest the rough beginnings of the beautifully regular striae found on the hairs of the inner pitcher surfaces. There are three hairs to a field.

The epidermal cells of *S. purpurea* (Pl. III, fig. 8) are more rounded wavy in outline than in *S. flava*. The stomata are more numerous, 16–17 appearing in a field. The glands are but slightly more frequent than above, 1.5 to a field. The hairs are straight, and vary in size even more than in *S. flava* .1, .2, .3, .4, etc., to .5–.6 mm. They are not quite so numerous as the hairs of *S. flava*, only two to an average field.

S. Catesbaei (Pl. III, fig. 10) shows epidermal cells more closely resembling *S. purpurea*. The stomata are fairly intermediate in number—11 per field. There is one gland per field about as in the parents. The hairs, of course, inherit the tendency to variability. Some hairs have the marked *S. flava* tendency to bending, though not so strong. On the whole, the range of size is much as in *S. flava* from .1 to .3 mm. There is one hair per field, less than in either parent.

Inner Lid Region

The epidermal cells of the inner portion of the lid are in all cases irregular in shape. In *S. purpurea* they are about as long as broad (.065×.05 mm.) with very wavy wall.

In *S. flava* the hairs are numerous, and compress the epidermal cells without hairs into oblong cells (.05×.03 mm.) with walls but slightly wavy. *S. Catesbaei* shows cells resembling *S. purpurea* in size and shape (.06×.047 mm).

Stomata are frequent on this surface. In these three forms they are of the same size, .035×.030 mm. In number they are noteworthy, *S. flava* having seven to a field, *S. purpurea* three, and the hybrid shows an intermediate number—five.

Glands are numerous over this, the alluring, surface. In *S. flava* there are 3–4 glands per field, in *S. purpurea* 2–3. The hybrid averages less than three.

This region is beset with more or less numerous long, stiff hairs, directed downward. These prevent the insects from pursuing any path other than that to the treacherously smooth conducting surface. The hairs are thickened in parallel ridges, varying in number according to the species.

In *S. flava* (Pl. IV, fig. 16) the hairs seem to be remarkably uniform in length. Measurements show that over 50% are .22 mm. long, while the remainder are .11 or .3 mm. in length. They are very numerous—10–11 to an average field.

S. purpurea (Pl. IV, fig. 15) has hairs many times longer than in *S. flava*. Besides these, there are shorter hairs, but none as short as the longest hairs of *S. flava*. They vary—about 50% are 1.3 mm. long, 20% are .6–.9 mm. in length, and the remainder are 1.8 mm. long or measure .9–1.0 mm. They are quite scattered, one hair base appearing in two fields.

S. Catesbaei (Pl. IV, fig. 17) has a variety of hairs, as has *S. purpurea*. Some are short, resembling those of *S. flava*, .2 m. long, while others approach the *S. purpurea* type—1 mm. long. Over 50% are less than .4 mm. in length; 20% are .5–.6 mm. long; the rest measure fom .7 to 1 mm. Hairs of the length of both parents are represented, since the shorter hairs of *S. purpurea* are .9–1 mm. in length, but by far the larger number of hairs are closer to the *S. flava* type. There are but two hairs per field.

The lower part of the tube, representing the conducting surfaces in *S. flava* and *S. Catesbaei*, and the glandular surface of *S. purpurea*, has an exterior epidermis of cells of the same character as those of the exterior of the lid. Hairs of the same character are present, but more infrequent than on the lid. These hairs point upwards, generally, toward the pitcher mouth, and become more numerous on the upper portion of the tube.

Stomata are very numerous over this surface. In *S. flava* and *S. purpurea* there are 14–15 stomata to a field; in the hybrid

fewer—10–11. The glands present have a tendency to be distributed along the strong ridges above the veins, especially in *S. flava*. Averages of counts from the surface between the veins run about .5 gland per field, while on the veins 2–3 glands appear in a field. In *S. purpurea*, where the veins are not so emphasized, the glands are equally distributed over the outer surface, and there are two to a field. In *S. Catesbaei* there are fewer glands than in *S. flava*—one to a field, though here there is a slight tendency for the glands to be more numerous over the veins.

The ridges spoken of above are formed by the reinforcement of the larger bundles on their inner and outer faces with a deep sclerenchymatous development. Above such bundles the subepidermal and epidermal layers become thickened enormously, so that the whole thickened area stands out above the surrounding epidermis. The ridges are very marked in *S. flava*, are not shown in *S. purpurea*, and are fairly conspicuous in *S. Catesbaei*.

The epidermis above the bundles undergoes a peculiar transformation. In *S. purpurea*, the wavy walled epidermal cells become elongated above the bundles. In *S. flava*, the epidermal cells are elongated, straight walled cells, much thickened. *S. Catesbaei* has these cells elongated slightly, heavily thickened—in fact about intermediate in character. Along these lines of cells there are no stomata, nor hairs; therefore they form the easiest paths which the insects can pursue upward toward the rim of the pitcher.

Conducting Surface

Below the lid surface in all forms, the epidermal cells become gradually polygonal in shape, and the hair processes become shorter and sharper. Every cell becomes prolonged into a pointed projection directed downward. The cells thus form a scale-like slippery covering for the inner pitcher surface to a varying depth. In *S. purpurea* it forms a narrow band, 1–2 cm. wide; while in *S. flava* and *S. Catesbaei* it extends over at least one-half of the pitcher depth.

The conducting cells of these three forms are interesting in length relation. In *S. purpurea* the tip process is but little more than a knob (Pl. V, fig. 22) and the cell measures .05 mm.

to the end of the projection. *S. flava* has a long, fine tip (Pl. V, fig. 23) and the cell measures .07 mm. in length. The upper portion of the conducting surface of *S. Catesbaei* shows an exactly intermediate size .06 mm. (Pl. V, fig. 24). These cells are all beautifully thickened with striae, as are the lid hairs.

L. S. Pitcher Rim

A longitudinal section through the rim of the pitcher mentioned above shows an interesting relation. In *S. purpurea* the rim is rolled outward and under, in two turns. In *S. flava* the rim is rolled over once, rather loosely. *S. Catesbaei* is rolled over, and slightly curved around again, or is rolled once and half.

The tip region in *S. purpurea* has three layers of thickened cells, while in *S. flava* the whole tip region is thickened. *S. Catesbaei* shows about an intermediate amount of thickening.

The conducting cells, with their fine processes, do not begin to show in *S. flava* at the tip, but considerably below the tip on the outwardly rolling portion.

Below the conducting cells in *S. purpurea* there are two layers of thickened cells, closely united to each other and to the epidermis. In *S. flava* there is but one such layer. In *S. Catesbaei* there is one regular continuous layer adjoining the epidermis, and a second discontinuous layer below it. The mesophyl in *S. purpurea* is loose, with large thin-walled cells. *S. flava* has a more compact and more shallow tissue than in *S. purpurea*. The mesophyl in *S. Catesbaei* is not so loose as that of *S. purpurea*, nor so compact as that of *S. flava*.

The outer epidermis in all three forms is composed of thin-walled cells. The stomata have their guard cells raised above the level of the epidermis in all three.

Below the outer epidermis is a region of regular large, thin-walled cells closely applied to each other. These cells form a false palisade tissue in the pitchers. In *S. flava* there are 3–4 layers of these cells; in *S. purpurea* 2–3 layers; in *S. Catesbaei* there are 2 layers. These cells contain numerous chloroplasts, and form a continuous layer, except where interrupted by stomatal chambers.

In *S. purpurea*, below the narrow conducting surface there is a wide expanse of glandular surface, reaching down to the

detentive. This region, absent in *S. flava*, is characterized by large regular wavy-walled cells with numerous glands—6.6 per field. These cells are smooth, without a suggestion of any hair process. The lower conducting area in the hybrid represents a crossing of the lower conducting area of *S. flava* with the glandular area of *S. purpurea*. There is no marked difference between the upper and lower portions of the conducting surfaces in the hybrid, excepting for a tendency toward lengthening of the cell process, and for the presence of numerous glands.

On the upper conducting regions of *S. flava* there are 3 glands per field; in *S. purpurea* there are 4 per field; in *S. Catesbaei* 2.9 per field in this region. The lower conducting surface in *S. flava* is devoid of glands; the glandular surface of *S. purpurea*, as has been mentioned, has 6 glands per field; in the hybrid there are 3, about half as many as are on the glandular area in *S. purpurea*.

The lengthening of the cell process noted above for the hybrid in this region may be due to the influence of the *S. flava* type of conducting cells, or merely be the exhibition of the tendency shown in all forms for the conducting cell process to become prolonged deep in the pitcher.

In the extreme lower conducting and upper detentive surface, the hybrid presents an interesting condition. This region, which represents a crossing of glandular-detentive area of *S. purpurea* with conducting-detentive of *S. flava*, exhibits a most confused zone about 1–1.5 cm. wide. There are several types of cells shown in this region:

First, normal conducting cells which become gradually elongated and give place to detentive surface cells.

Second, cells intermediate in size and shape between the glandular surface cells of *S. purpurea*, and the detentive surface cells of *S. flava*. These are long narrow cells with wavy walls. They appear at first isolated as islands of two or more cells, in the lower conducting surface; becoming more numerous below, and gradually giving place to normal detentive-surface cells. These cells represent a blending of the glandular surface cells of *S. purpurea*, with the unmodified epidermal cells of the detentive surface of *S. flava*.

Third, normal detentive surface cells, polygonal in shape, some bearing long hair processes. These appear isolated in

the region where the blended detentive-glandular cells are most numerous.

Fourth, normal glandular cells of *S. purpurea*. These cells are reproduced in patches, isolated, in the region of the detentive-glandular cells.

Fifth, normal detentive epidermal cells with or without hair processes, intermediate between the types of *S. flava* and *S. purpurea*.

Sixth, normal glands; two per field. These occur down to the purely detentive zone, where they cease.

A similar case, such as above, is presented in a hybrid between *S. minor*, without a glandular area, and *S. purpurea*, and has been discussed shortly by Macfarlane (28). He considers that this region represents a modification of the upper detentive surface. In both hybrids it seems to be shown that the conducting-surface cells of one parent are incapable of blending with glandular surface cells of *S. purpurea*, since no wavy-walled cell with a prolongation characteristic of the conducting surface type ever appears. In other words, this represents a clear case of the so-called bi-sexual hybrid (29), or of particulate inheritance (38).

The detentive surface presents no such confused condition, rather a perfect blending, cell for cell. In this region, in these forms, there are no stomata nor glands present. In all, the epidermal cells are polygonal and contain a fair amount of tannin (30). The hair cells are remarkable in relation. In *S. purpurea* they are long—1.5 mm.—and rather infrequent—.7 to a field. Those of *S. flava* are quite short—.37 mm.—but very numerous—5.5 per field. In *S. Catesbaei* the hairs are intermediate in size and number, for they are .88 mm. long, with 2.8 per field.

Lower Pitcher Region

T. S. of pitcher at lowest part of tube shows in all a hollow cylindrical portion, representing the T. S. of the pitcher proper. From the front extends the more or less wide wing, representing the fused laminae (23). In the cylinder the bundles are disposed at intervals, larger and smaller alternating, with the xylem on the inner side, toward the pitcher cavity. In the wing, two rows of bundles face each other, xylem opposed to

xylem. The things especially to be noted in comparing parents and hybrids are: the number of the subepidermal layers of cells, the depth and character of the mesophyl tissue, the relative amount of sclerenchymatous tissue developed on the inner and outer side of the bundles, the number of subdetentive layers.

In all three forms, the outer epidermal cells are regular with heavily cutinized walls. The stomata have their guard cells slightly raised above the epidermal level.

Below this are the subepidermal layers of cells rich in chloroplasts, forming on the morphologically lower surface a false palisade. In *S. purpurea* there are 3–4 layers of cells, large and thin-walled. In *S. flava* there are 4–5 layers of these cells. They are smaller and more compactly arranged. *S. Catesbaei* resembles more *S. purpurea* in that there are three subepidermal layers, which have larger cells less compactly arranged than in *S. flava*.

The mesophyl is in *S. purpurea* deep and loose. The cells are large, and intercellular spaces are frequent. *S. flava* has a very narrow mesophyl zone. The cells are regularly arranged with few intercellular spaces. In *S. Catesbaei* the mesophyl is deep and spongy as in *S. purpurea*. In the mesophyl the bundles are distributed. In *S. purpurea* they are not strongly reinforced with sclerenchyma tissue. In *S. flava* the reinforcement is pronounced, and involves the subepidermal and epidermal layers as well in the larger bundles. In *S. Catesbaei* the development is about intermediate between the parents.

There are two or more layers of cells below the detentive surface which are thickened together with the epidermis. It is this which forms the so-called "absorption zone" mentioned by Fenner (31) and others. The contents of these cells are either gathered into large masses, or broken up into finely granular substance. These layers give a strong positive reaction for tannin. In *S. purpurea* there are 1–2 layers of subdetentive cells. In *S. flava* there are two layers. In *S. Catesbaei* there are three layers.

Set 2. S. flava, S. Drummondii and S. Moorei

The second hybrid of the series, between *S. flava* and *S. Drummondii*, was the first artificial hybrid between species of Sarracenias to be exhibited. Though it was named in honor

of its exhibitor, Dr. David Moore (21), it was also widely known as *S. Mandaiana*, which name was applied to the natural hybrid.

Both parents are strong and beautiful types, and as one might expect, as already noted in Dr. Moore's paper, quoted above, the hybrid is also a striking form. It is intermediate in appearance between the parents where the parental characteristics are capable of blending; but exhibits an apparent marked divergence toward one parent where a single characteristic can be inherited. This is particularly noteworthy in the pale areas on the lid and tube of *S. Drummondii*.

S. Drummondii (Pl. I, fig. 4) is, like *S. flava* (Pl. I, fig. 2), tall, strong, erect, with pitchers ranging from 30–90 cm. high. Average specimens usually measure 60–70 cm. *S. flava*, it will be recalled, is about of the same height. *S. Moorei* (Pl. II, fig. 5) is about 65–70 cm. high.

In both parents and hybrid the pitchers are slender below, increasing gradually in width to the flaring rim. The pitchers of *S. flava* seem on the whole to be more robust than those of *S. Drummondii*, and the hybrid seems to resemble *S. flava*, or to be even stronger.

The wing is narrow in these three forms. In *S. flava* it continues undiminished up to the rim, while in *S. Drummondii* it narrows down to a mere ridge some distance below the rim. *S. Moorei* has the wing narrowing down to a mere ridge, but closer to the rim than in *S. Drummondii*.

The lids in these types form an interesting series. That of *S. flava* is ovate-cordate, with a strong median process, and a straight margin. *S. Drummondii* has an orbicular lid with a blunt apex, and a wavy margin. In *S. Moorei* the lid is nearly intermediate between ovate and orbicular, with a slightly wavy margin, and a tip process not so pronounced as in *S. flava*.

In color relation the hybrid is remarkably intermediate. The typical *S. flava* is pale green, excepting for the red throat marking. (Variations: purplish-veined lid, or with an entirely purple pitcher.) The pitchers in *S. Drummondii* are green below with white areolations over the lid and upper tube; the areas between the areolations are marked with red veinings. Ruddy forms of this occur. Not uncommonly there is a pale form with green pitcher below, while, above, the areolations

are so enlarged that they become confluent, and the whole upper portion appears dazzling white. To this variety has been given the name *alba*. The typical hybrid shows a green pitcher with white areolations over the lid and upper tube; together with the red throat of *S. flava*, which is here lessened in intensity. There is also a hybrid (11) noted with the white variety of *S. Drummondii* named above. In it the hybrid is pale, with pronounced areolations, as in *S. Drummondii*. Where the ruddy varieties are crossed the hybrid is very beautifully colored. The throat and rim are velvety red, with white areolations and crimson veining over the lid and pitcher.

Outer Surface of the Lid

The outer epidermal cells of *S. Drummondii* (Pl. III, fig. 11) are slightly angular-rounded in shape. The cell walls project upward into a slight rounded papilla. This has been noted by Macfarlane (28). The stomata are grouped in special tracts above the veins between the areolations on the lid. The glands are more numerous over this special region also, but are sparsely scattered over the entire surface. The hairs are short and blunt above the veins. Around the window areas the hairs are longer.

In *S. flava* the cells are longer than broad, with wavy walls. The surface of the epidermis is flat, the hairs, stomata, and glands are quite evenly distributed over the entire surface of the lid. There is no suggestion of grouping of the stomata in any special region.

The epidermal cells in the hybrid (Pl. III, fig. 12) are squarish, with slightly wavy walls. There is very little or no swelling of the upper cell surface. The stomata are distributed in tracts, but these areas are wider, and the stomata are less closely grouped. There are spaces devoid of stomata as in *S. Drummondi*, where the glands are sparsely distributed. The hairs are long and strong over these areolations.

Inner Lid Surface

On the inner surface of the lid of *S. Drummondii* (Pl. IV, fig. 18) the cells are wavy walled, measuring .06 × .05 mm. to .05 × .04 mm. See Pl. IV, fig. 16 for the appearance of the lid cells of *S. flava*, already described above in detail. The cells of the lid of the hybrid are intermediate in shape (Pl. IV, fig. 19).

The stomata, as in the case of the previous hybrid, form an interesting series. *S. flava* has 7.25 per field, while *S. Drummondii* has very few—only .59 per field. The hybrid is intermediate, with 3.4 per field. The size of the stomata varies in these forms. In *S. flava* they are .035 by .03 mm., in *S. Drummondii* they are large, .045 × .04 mm. In the hybrid the size is intermediate—.04 × .035 mm.

The glands present the same curious phenomenon as before; that is, there are fewer in the hybrid than in either parent. *S. flava* has 3.4 per field, *S. Drummondii* 4.2, while *S. Moorei* has but 2.4.

The hairs of *S. flava* vary from .1 mm. to .3 mm., with .2 mm. as the average length. *S. Drummondii* has remarkably long, fine hairs. There are present besides small fine hairs. The length varies from 1.98 mm. in length to .44 mm. The average length is about 1.07 mm. with 1 per field. As in the former hybrid considered, *S. Catesbaei*, the *S. flava* parent exerts strong influence on the size of the hairs. The hairs of *S. Moorei* vary greatly in length; very few are over 1 mm. long, however. The average length is about .5 mm.; which is close to intermediate between the species. They are more frequent than in *S. Drummondii*, 2.3 per field, which is many times less than the hairs of *S. flava*. It seems that there is an inability in the hybrid to reproduce to any extent the numerous hairs of the *S. flava* type.

Conducting Surface

The conducting surface in these types reaches to the detentive surface without interruption. In *S. flava* (Pl. V, fig. 23) the cells were .07 mm. long, with a tip process .03 mm. in length. In *S. Drummondii* (Pl. V, fig. 25) the tip is longer, .05 mm. in length, while the whole cell measures .15 mm. In the hybrid (Pl. V, fig. 26) the cell is .11 mm. long, with a tip intermediate in size, .04 mm. The glands are grouped more abundantly over the upper conducting region, about the rim, and immediately below. Below this nectariferous area, the glands become less frequent and cease entirely over the lower half of the conducting surface. In *S. Drummondii* there are 3–4 per field in this upper area; in *S. Moorei*, 4 or more. In *S. flava*, where the glands are not so limited in distribution, there are 3 per field.

Longitudinal Section of the Rim

A longitudinal section through the rim region of *S. Drummondii* shows that the rim is rolled over once as in *S. flava*, but with no trace of the peculiar flattening on the under part of the turn. The tip is in *S. Drummondii* pointed and elongated, with thickened cells through the whole tip. The conducting cells do not appear until well around the outer curve of the rim; while in *S. flava* they occur at the outermost edge of the rim. In *S. Moorei* they appear further around the rim than in *S. Drummondii*. The tip region of *S. Moorei* is not so pointed as in *S. Drummondii*, nor as blunt as in *S. flava*; it is between the two.

There are in *S. Drummondii* two rows of thickened cells subjacent to the conducting epidermis. *S. flava* has only one row of such cells, while in the hybrid there is a complete row, and a second incomplete row.

The mesophyl of all three types is compact, excepting for the regions of the areolations in *S. Drummondii* and *S. Moorei*. Here the tissue is loose, with many air spaces. In *S. Drummondii* the cells of these areas are devoid of contents, but the tissue of this region is as deep as that of the non-etiolated portions. In *S. Moorei*, in young leaves, these areas are not entirely devoid of chlorophyl, so that they appear light green rather than pure white as in *S. Drummondii*.

Below the mesophyl there is in *S. Drummondii* a reversed palisade of 3–4 layers of cells; in *S. flava* there are 3–4 layers; in *S. Moorei*, 3 complete and regular layers.

The outer epidermis of *S. Drummondii* is swollen into peculiar pointed papillae. These become especially pronounced over the areolations. *S. flava* has a smooth epidermis, but in *S. Moorei* a trace of such swellings as are present in *S. Drummondii* occur. They are here more rounded than in *S. Drummondii*.

Detentive Surface

On the outer part of the conducting and upper detentive areas of *S. Drummondii* there are stomata present. They are very sparsely scattered and rather difficult to find. About them is a group of special cells. In counting a hundred fields for detentive hairs, four such stomata were found. In *S. Moorei*,

two stomata were found in a hundred fields. The number here is perhaps not to be taken as an average; but one may confidently assert that there are fewer stomata present in the hybrid than in *S. Drummondii,* although they may or may not be intermediate in number.

The hairs of the detentive surface are about as numerous in *S. Drummondii* as in *S. flava*, 5–6 per field. In *S. Moorei* the hairs are more numerous—7–8 per field. In length, as before, the hybrid is intermediate: *S. flava* .37 mm. long, *S. Drummondii* .54 mm., *S. Moorei* .45 mm. The epidermal cells from which they spring are straight walled cells, characteristic of detentive surfaces.

Outer Epidermis of the Pitchers

The epidermal cells of the outer surface of the pitcher tube are swollen as on the upper lid portion; excepting over the region of the veins, where straight walled, much thickened cells take their place. Stomata are very numerous, 10 or more to a field; glands are infrequent, one to a field; and hairs are absent. In *S. Moorei* the epidermal cells are slightly swollen; the stomata are more numerous than in *S. Drummondii*, 12 per field; glands are 1–2 per field; no hairs are present, as in *S. Drummondii.*

T. S. Tube at Base of Pitcher

The cells of the outer epidermis of *S. Drummondii* are so swollen that the stomata appear sunken, instead of raised above the epidermal level as in *S. flava.* There are here but three layers of false palisade. The mesophyl is deeper and looser than in *S. flava* with peculiar bands of cells rich in contents forming a complete ring about the pitcher tube. There are two layers of sub-detentive cells, with tannin present.

The tube sections of *S. Moorei* resemble those of *S. Drummondii* closely because of the presence here also of the peculiar bands of parenchyma cells in the mesophyl region. There are two layers of reversed palisade, and two rows of subdetentive cells with peculiar aggregated contents, noted above in *S. flava.*

The "ridges" above the veins are more pronounced in *S. Drummondii* than in *S. flava. S. Moorei* shows an intermediate amount of thickening in this region.

Set 3. S. Sledgei, S. Drummondii, and S. areolata

S. Sledgei (Pl. II, fig. 6) has an upright, slender pitcher, slightly inflated in its upper half, slightly constricted at the rim. Average pitchers are 55–65 cm. high. The pitcher of *S. Drummondii* (Pl. I, fig. 4), it will be remembered, increased gradually in width, up to the rim. *S. areolata* (Pl. II, fig. 7) is about as high as *S. Sledgei*—55–65 cm. The rim is not constricted as in *S. Sledgei*, nor is it so expanded as in *S. Drummondii*. The fused lamina extends but little in these three forms. It is about 4 mm. wide in *S. Sledgei*, while in *S. Drummondii* it is very narrow—only 2 mm. wide. *S. areolata* shows it about as in *S. Drummondii*, or slightly wider.

The lid in *S. Sledgei* is ovate-cordate, with a straight margin. In its median portion it is prolonged into a tip. *S. areolata* shows a lid intermediate in shape between the ovate lid of *S. Sledgei*, and the orbicular frilled lid of *S. Drummondii*. There is a slight tip process.

The pitchers of *S. Sledgei* are green, veined with crimson over the upper portion and the lid region. There is also a ruddy variety with deep crimson lid and upper tube. *S. Drummondii*, of the type described as one of the parents of *S. Moorei*, has a green pitcher marked on the lid and upper tube with white areolations and reddish veinings. *S. areolata* has more pronounced reddish purple vein markings than *S. Drummondii*. The white areolations are reproduced over the upper lid and pitcher areas, but are fainter than in *S. Drummondii*. Where the *S. Drummondii* parent is of the *atropurpurea* type, the hybrid is very richly colored with purple lid and white markings.

Outer Lid Surface

In *S. Sledgei* (Pl. III, fig. 13) the epidermal cells are longer than broad, with angular walls. There are numerous stomata distributed equally over the epidermal surface, averaging six to a field. Glands are sparse—one to a field on this outer surface. There are but few hairs, and these are extremely short. In *S. Drummondii* (Pl. III, fig. 11) the cells are rounded, swollen; glands and stomata are distributed in limited areas between the areolations. In the hybrid (Pl. III, fig. 14) the epidermal cells are inclined to have rounded walls, slightly swollen into

papillae. The stomata and glands are grouped in special tracts as in *S. Drummondii*, but they are wider and less well defined. There are strong hairs scattered abundantly over the lid surface, especially around the margins of the window areas. They are much stronger than in either parent.

Inner Lid Surface

The epidermal cells of the inner lid surface of *S. Sledgei* (Pl. IV, fig. 20) are longer than broad, and wavy-walled. In *S. Drummondii* (Pl. IV, fig. 18) they are about as long as broad, with walls slightly wavy. *S. areolata* (Pl. IV, fig. 21) has cells remarkably intermediate in size and shape.

Stomata are sparsely distributed over the inner lid region of *S. Drummondii*, where the average per field is .59. In *S. Sledgei* they are quite abundant—3–4 per field. In the hybrid they are quite intermediate in number—2–3 per field.

The hairs of the lid in *S. Drummondii* are variable in length. They exceed in their greatest length the hairs of *S. purpurea*, reaching almost 2 mm. in length, while the shorter ones are only .3 mm. long.

In *S. Sledgei* on the other hand the hairs are of a uniform length. They are stout and short, varying slightly from .55 to .88 mm. long. None are as short as the shorter of those of *S. Drummondii*, .3 mm. In *S. areolata* the hairs vary greatly in length after the fashion of the *S. Drummondii* parent. There are hairs present as short as the shortest of *S. Drummondii*, but the longest hairs are a little over half as long as the longest hairs of *S. Drummondii*—1 mm. Hairs .7–.9 mm. in length are the most numerous. That is the influence of the *S. Drummondii* parent is shown in the tendency to wide variation in length, and in the lengthening of all of the hairs. The glands in the three forms are fairly numerous—4 in *S. Drummondii*, 4 in *S. Sledgei*, and 4 in *S. areolata*.

Conducting Surface

Conducting surface cells here do not show the exact relation shown in the other hybrid. In *S. Drummondii* (Pl. V, fig. 25) the cells were large and measured .15 mm. in length. In *S. Sledgei* (Pl. V, fig. 27) the cells are about .09 mm. long, and are narrow and oval in shape. In *S. areolata* (Pl. V, fig. 28) the cells are of the same length as in *S. Sledgei*, but are wider and in shape are halfway between the parent forms.

The glands in these three forms are most numerous about the pitcher rim, and quickly lessen in number one inch or so below the rim. They are scattered sparsely for a short space below, but cease entirely beyond the upper one-third of the conducting surface. In *S. Sledgei* the glands are remarkably numerous, 7–8 per field over the upper region, near the rim. In *S. Drummondii* they are more infrequent and average 3–4 per field. In the hybrid there are almost as many as in *S. Sledgei*—6–7 per field. In the extreme lower portion of the conducting surface in all three forms are stomata scattered very sparsely, set in a group of special cells.

Longitudinal Sections of the Rims

The rim of *S. Sledgei* is rolled over once in a rather loose turn. The tip is blunt with several thickened cells. The conducting cells appear about halfway round the outward turn. Beneath the conducting cells is a single layer of subepidermal cells. The mesophyl is deep and loose. There are two layers of cells forming a false palisade below the epidermis.

In *S. Drummondii* there are two sub-conducting and 3–4 subepidermal layers. The mesophyl is loose, especially below the areolations.

In *S. areolata* the rim is intermediate. Beneath the conducting cells are two layers of subepidermal cells. The mesophyl is deep and loose especially below the window areas. Beneath the outer epidermis are three subepidermal palisade layers.

Detentive Surface

The detentive surface of *S. Drummondii* is, as has been described above, composed of normal straight-walled polygonal epidermal cells. A few normal stomata are scattered over this surface, but no glands are present. Hairs are present, of the normal variety, .8–.9 mm. long, 3–4 to a field.

In *S. Sledgei* this surface departs from the normal detentive in that some of its cells are wavy walled, with very different contents from those of the detentive epidermal cells. These cells appear only on the upper detentive area in large groups isolated in the midst of characteristic detentive cells. Other cells show all transitions between straight walled detentive surface cells, and isodiametric wavy walled cells resembling

closely the glandular surface cells of *S. purpurea*. In fact the whole area has much the same character as the corresponding area in the hybrid *S. Catesbaei*, excepting that none of these cells appear as intrusions among the conducting surface cells, and that they extend deep into the detentive surface. The writer infers the probability that this region represents a primitive glandular surface.

On the normal detentive surface the hairs are short, .3–.4 mm. in length, but numerous, 7–8 per field. The hybrid possesses a normal detentive surface with polygonal cells and no glands. Stomata are present. The hairs are intermediate in size and number. They are .6–.7 mm. long, with 5–6 per field.

Transverse Sections of Tube

S. Drummondii, as has been previously noted, shows in transverse sections of the tube-base epidermal cells swollen into papillae; below these, two subepidermal layers, a loose mesophyl, and 1–2 subdetentive layers occur.

In *S. Sledgei* the epidermal cells are oval. Below them are three layers of subepidermal cells. The mesophyl is loose with many air spaces. The mesophyl cells contain the same peculiar contents noted in the section of *S. Drummondii*. In this form however the cells so supplied are arranged in a continuous layer in the mesophyl tissue, below the false palisade tissue. There are 1–2 layers of sub-detentive cells.

In *S. areolata* there are two layers of subepidermal cells; and two layers of sub-detentive cells. The mesophyll is loose as in both parents. There is a suggestion of the peculiar bands of special storage cells, as in the case of *S. Sledgei*, though the layers are not continuous.

Flowers

S. flava, *S. purpurea*, *S. Catesbaei*

The flower of *S. flava* is pendulous and measures 7 cm. in length, 13 cm. across. Those of *S. purpurea* are smaller, 4–5 cm. long and 9 cm. wide. In specimens at hand of *S. Catesbaei* the flowers are intermediate in size, 5–6 cm. long and 10–12 cm. wide. Other specimens seem to point to a greater robustness in it than in either parent.

The bracts in all three are small, covered with honey glands and a few stomata. The glands are distributed over the central

part. In color, in *S. flava* they are yellowish membranous, with green veinings. Those of *S. purpurea* are reddish, or green with a reddish margin. In *S. Catesbaei* the bracts are reddish with a green tip.

The sepals of *S. flava* are 4 cm. long by 3 cm. broad. They are ovate and greenish yellow. Stomata are frequent, and the numerous glands are massed towards the edges and tip of the sepals on the outer side. On the inner, or morphologically upper, surface the glands and stomata are less frequent than on the outer side, but distributed in the same manner.

In *S. purpurea* the sepals are 3 cm. long, ovate as in *S. flava* and red in color. Glands are not so numerous as in *S. flava*, but distributed along the margins as above. The sepals of *S. Catesbaei* are 4 cm. long, ovate, green tinged with rosy pink, or with red veinings. Glands and stomata are more numerous than in *S. purpurea*, distributed as before.

The petals in *S. flava* are 7–8 cm. long, with the proximal portion not wider than the distal expanded part. The expanded portion at its lower third forms a cuneate tip characteristic of *S. flava*. In color the whole petal is a flavous yellow, the pigment being due to yellow chromoplasts. The constricted por-

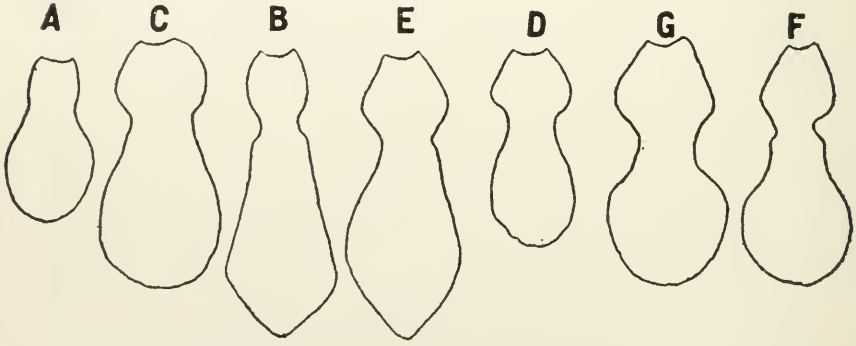

Fig. 29. Outline drawings of petals of *Sarracenia* flowers × ½. See text for description.

tion of the petal (fig. 29, B) is rolled over rather deeply. Glands and infrequent stomata are distributed alightly behind the tip of the petal, and along several of the median veins. At the region of the constriction they become very numerous. In this area too, the epidermal cells become swollen into rounded

papillae. Above the constricted area there are no stomata, nor glands, nor papillate swellings. On the inner surface, the distribution of stomata and glands is practically as above, excepting for the presence of several rather long, fine hairs along the median veins of the constricted area. *S. purpurea* has petals 4–5 cm. long. The proximal portion of the petal is not wider than the distal section. The constriction between them is very shallow (fig. 29, A), and the sides of the petals scarcely rolled back. The distal portion of the petal is ovate. In color, the petal is crimson without, much lighter within. The base of the petal is pale greenish or whitish. Glands are numerous over the central part of the petal, back as far as the constriction. In *S. Catesbaei* the petals are intermediate in length, 5–6 cm. long. The upper portion is slightly more rounded than in *S. purpurea;* the constriction is more pronounced than in the latter (fig. 29, C). The color is intermediate. Above, the petal is white. The lower portion of the petal is rose-pink. That is, the purple-pink dissolved pigment in *S. purpurea* is diluted and weakened by the chromoplasts from *S. flava*. Glands are present at the tip, and along the median veins only to the constricted areas.

The stamens in all are variable in number—from 50–60. They are formed by the breaking up of each of the 10 staminal primordia into 5–8 lesser primordia.

Pistil. The umbrelloid style is provided with numerous long hairs, pointing generally toward the 5 stigmatic knobs. The stigmatic hairs are short and stout, usually bent with the tip often swollen.

In *S. flava*, the stigmatic hairs are short and but slightly curved, with swollen tip.

In *S. purpurea*, the hairs are longer, and more decidedly curved. The hairs of *S. Catesbaei* are longer than those of *S. flava*, yet not so long as those of *S. purpurea*. The stylar hairs are abundant and long in *S. flava*. In *S. purpurea* the hairs are of about the same length, sparse within, absent without. In *S. Catesbaei*, however, the hairs are very short.

S. flava, S. Drummondii, S. Moorei

In *S. Drummondii*, the flowers are pendulous, as in *S. flava*, are of about the same size, 6–7 cm. long, and 14 cm. across their greatest width. The bracts are red. *S. Moorei* has usually,

at least in all the greenhouse specimens, a larger flower than those of the parents. They are 7 cm. long and 13–15 cm. across. The bracts are reddish green.

The sepals are deep crimson in *S. Drummondii*, ovate in shape, measuring 4–5 cm. in length. Those of *S. Moorei* are of like size, but show an intermediate coloring and shape. They are reddish pink above, and yellow beneath, and are rather narrower than the sepals of *S. flava* (35). Stomata and glands appear as before at the tip and along the sides of the sepals.

The petals are interesting in relation in this series. They are 6–7 cm. long in *S. Drummondii* (fig. 29, D) and have a basal segment which is rhomboidal in shape, and much wider than the "banner" below. The margin of the petal is rolled back strongly at the constriction; the banner portion is oval in shape and the whole petal is colored a rich deep crimson, due to a dissolved crimson pigment, except at the extreme base, where the petal is green. The epidermis of the petal, like the outer epidermis of the pitcher, is swollen into papillae, which become especially prominent in the constricted area. There are few glands scattered at the lower part of the petal, and up the median veins. There are none in the constricted area of the petal, where they are so numerous in *S. flava*.

In *S. Moorei* (fig. 29, E) the petals are intermediate in color and shape. The basal portion is wider than in *S. flava* and narrower than in *S. Drummondii*. The lower portion of the petal is pointed, somewhat suggesting the cuneate tip of *S. flava*, but rounds out above more like *S. Drummondii*. In color the petals are light at the base—a yellowish green, becoming a peculiar maroon color below the base on the outer side of the petal and yellow within, due to combined crimson dissolved pigment and yellow chromoplasts of *S. Drummondii* with the yellow chromoplasts of *S. flava*. The glands are less numerous than in *S. flava*, but are distributed in the same way, toward the tip, up the median veins and over the constricted area.

In *S. Drummondii*, the style is flushed with crimson over its outer surface; while in *S. flava* it is yellow. In *S. Moorei* the style is yellowish, with faint red markings.

The hairs of the umbrelloid style of *S. Moorei* are longer and stronger than those of the parents.

S. Drummondii, S. Sledgei, and S. areolata

The flowers of *S. Sledgei* are nodding, but the petals are spreading in this form, instead of drooping and hanging out as banners, as in the other types so far considered. They are rather large and showy, 5–7 cm. long, 11–14 cm. wide. Those of *S. areolata* exhibit somewhat the same spreading habit as in *S. Sledgei*. The flowers are 5.5–6 cm. long, 13 cm. across.

The bracts in *S. Sledgei* are pink with a greenish tip; those of *S. areolata* more red, due to the *S. Drummondii* parent.

The sepals of *S. Sledgei* are greenish, fading to yellow. They are ovate with blunt tips and measure 3–4 cm. long. Those of the hybrid are longer, 4–5 cm., and are cordate in shape. They are greenish with a red margin. Glands are present on the tip and along the margins of the sepals.

The petals of *S. Sledgei* (fig. 29, F) are about 6 cm. long, with a wide basal segment, a deep constriction, and a much rounded "banner." They are pale lemon-yellow in color, fading to white. Glands are very sparsely distributed, one or two at the tip and several up the central vein. They do not appear above the constriction. As before, the cells of this portion of the petal, on the outer surface, are swollen into slight rounded papillae.

In *S. areolata* (fig. 29, G) the petals resemble *S. Sledgei* in that the shape of the banner is decidedly rounded. The basal portion is wider than in *S. Sledgei*, approaching to rhomboidal as in *S. Drummondii*. In color they are intermediate between the crimson of *S. Drummondii* and the yellow of *S. Sledgei*. The color is rather more rose-pink than red on the outer surface, while within the petals are pale yellow. There are no glands present on the petals, at the constriction. The epidermal cells are prominently papillate, though not so strongly as in *S. Drummondii*.

The umbrelloid style is pale yellow in *S. Sledgei*, while in *S. areolata* it is more greenish in color, with red veining.

The hairs of the inner side of the style are short, while in *S. areolata* they are remarkably long and strong, exceeding even those of *S. Drummondii*. The hairs of the stigma of *S. Sledgei* are short and curved, while those of the hybrid are longer and much less curved.

Glands

The structure of the glands on the pitcher surfaces, spoken of in this paper, is in general identical. Brief descriptions have been given, and several figures by Goebel (32), Fenner (31), and others. There are above, appearing on the epidermal surface, two central cells, heavily thickened, surrounded by from 4 to 6 companion cells. The cap cells, or the central cells, are wedge-shaped, and run down between the surrounding cells into the second or third tier of cells constituting the gland. The whole structure is then flask-shaped, and is composed of 16 or more cells, extending down into the mesophyl, but separated from that tissue by a cuticular lamella, with reticulate thickenings. The cap cells mentioned above stain differently from the surrounding cells, taking gentian-violet stain deeply, while the surrounding cells absorb safranin. Further, the surrounding cells give a marked positive reaction for tannin, with ferric iron chloride. In view of the above, it seems very probable that the cap cells are the secretory cells, and that the tannin present is the source for the sugar in the secreted liquid.

Though the structure of these glands has been considered briefly, there has been but one paper tracing their development—that of Fenner (31). He describes their origin from an epidermal initial cell which divides longitudinally and transversely to form a two-tiered group of cells. But next he considers that a split occurs between the upper cells, and that this split deepens until it involves the lower layer also. Into this "pit," he says, the secreted honey is poured. The writer finds no evidence of any such splitting. In fact the pit he mentions occupies the position of the cap cells. What occurs is this: The gland initial divides longitudinally and transversely as indicated, forming a two-tiered structure of four cells, two above, two below. From the two upper cells are cut off two smaller cells after the fashion of guard cells. These two cells are the cap cells. The two upper cells redivide to form the 4–6 surrounding cells. The second tier below divides transversely and longitudinally into 8–16 cells to form the second and third tiers. While this growth is going on, the two cap cells are pushed to a central position, and are flattened against each other until they assume the characteristic wedge shape (32).

Ovarian Gland Structure

The above description applies to the glands present on all the vegetative parts, as well as on the bract, sepals, the petals and umbrelloid style. But over the tubercles on the surface of the ovary are still more complex glands. Macfarlane (28) gives the following description of the nectar secretion: "The epidermal cells of the ovarian surface have undergone repeated divisions, and have swollen out into minute glassy beads or tubercles from which a quantity of rich nectar exudes before, during, and for some time after, blossoming. This, as we will show, is evidently of great use in the pollination of the flower." "When a flower has nearly opened the stamens begin to dehisce and as the blossom has a pendulous position the pollen from the stamens is showered down into the umbrelloid style-cavity below. But about this time the warted bead-like ovarian surface exudes large drops of sweet juice, which increases in quantity as the stamens continue to dehisce, till it oozes down among the filaments and anthers, washing with it the pollen-grains. It then accumulates in the umbrelloid cavity, and forms there a nectar-bath of pollen."

When serial sections of the ovarian wall of an opened flower are studied, the source of the abundant honey is seen to be in the large nectar glands situated at the bases, and along the sides, of the tubercles mentioned above by Macfarlane. The glands are more numerous over the tubercles of the lower half of the ovary. The tubercles over the upper surface of the ovary are devoid of glands. Following is an account of the mode of origin of the tubercles and glands:

In a very young flower, where the anthers show the pollen mother cell stage, the ovary is as yet very small, and its epidermis smooth. The ovarian tissue is, however, growing rapidly at this period, and division figures are frequent. They indicate a longitudinal division for the epidermal cells invariably, while in the subjacent tissue both longitudinal and transverse divisions are common. At this time both petals and sepals possess fully formed glands and stomata. The ovarian wall as yet shows no trace of either. The epidermis continues to divide more frequently than the tissue below. This excessive division is somewhat localized along the ovarian wall, so that there results here and there a slight swelling. The layer im-

mediately below the epidermis becomes differentiated also from the ovarian tissue. The cells become enlarged and filled with a peculiar content present in the epidermis also. This layer shows rapid division and pushes up into the swelling. It is impossible at this time to trace the gland initial cell. At this time, the pollen mother cells are in the anaphase of the first or heterotypic division.

As the epidermal cells divide, the swellings become more pronounced. Two subepidermal layers become involved. The outer cells of the tubercles become enlarged and oblong while the cells between the swellings become compressed and small. The first gland initials are found at this stage. They are usually situated at the base of the swellings and consist of one or two cells with a large nucleus and richly granular protoplasm. At this time the pollen grains are in the tetrad stage, and the megaspore mother cell is distinguishable.

The swellings become deepened as the flower matures and press together tightly so that they assume a squarish or oblong shape (fig. 30). At this time the glands are fully developed.

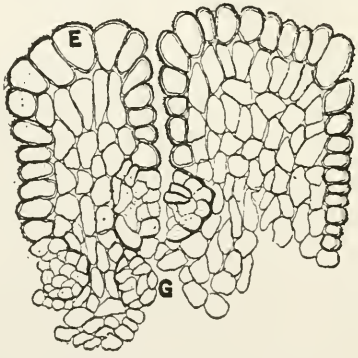

Fig. 30. Longitudinal section through mature ovarian wall, × 100. G = gland in section; E = epidermis with waxy layer on outer surface.

They have the same fundamental structure as the simpler glands on the leaves, etc.; that is, they possess a set of 2 or frequently 3–4 central cells running down into a mass of small cells below.

The gland is irregularly spherical in shape, and is composed of many more cells than the glands on the pitchers. There may be 60–80 cells concerned in the formation of the ovarian

glands. They lie embedded in the tissue of the papillae, for the most part at their base. The honey secretions are poured out into the tiny crevasses between the papillae, and are drawn upwards by capillarity to the lower part of the ovary, there to collect about the base of the filaments as has been noted by Macfarlane above.

The papillae, mentioned as being nectariferous (28) in themselves, are oblong masses of fundamental tissue. The outermost or epidermal layer and a subepidermal layer become enlarged, and regular, forming a noticeable bounding layer. These two outer layers contain a peculiar substance from the earliest stages of their differentiation. They have on their outer surface a coating of wax which gives with alkanna and Soudan III a characteristic reaction. The tissue of the papillae is richly supplied with oil globules. The contents of the cells of the bounding layers stain deep brown with iodine and potassium iodide, indicating perhaps that an alkaloid is present. Its position and abundance may indicate the presence of such a protective substance. An alkaloid has been mentioned as being present in the family by Porcher (34). *Sarracenin* was the name temporarily applied to it, and it was thought to have medicinal value for stomach troubles and smallpox. Such an alkaloid, however, is not mentioned in such a treatise as that of Winterstein and Grier. Several diagnostic tests for alkaloids were applied besides iodine in potassium iodide. Nitric acid on sections dampened with potassium hydroxide in alcohol gave a rather deep orange color, with here and there a decided pink tint in the bounding layers. No reaction occurred with platinic chloride. On adding ammonia, a decided bright green color was obtained.

In view of the fact that these papillae have their outer walls heavily thickened and covered with a protective waxy coating; and are supplied with abundant nectariferous glands over the lower portion, it is evident that the nectar is secreted by the glands and not by the papillae as a whole.

Conclusions

It will be seen from the above description that the hybrid forms, in comparison with their parents, are intermediate in relation in almost all details.

In size it has been shown that the hybrids are generally intermediate, though *S. Moorei* and *S. areolata* frequently incline to show a characteristic increase in vigor over the parent types.

In shape the intermediateness is particularly well shown in the first hybrid, *S. Catesbaei* (fig. 3), where the diverse shapes and habits of the two parents are so neatly blended. The parents of the other forms do not present so diverse an appearance; but in small details, such as the shape of the mouth opening, or the width of the fused laminae, the hybrid shows an intermediate character.

In all the blending of the parental lid shapes is shown. Where a form with a frilled margin—as in *S. Drummondii* or *S. purpurea*—is crossed with a form with a straight margin, the resulting hybrid has a lid with a frilled margin, but more loosely wavy than in the parent. When a form like *S. flava*, which has a median tip process on the lid, is crossed with a blunt tipped form like *S. purpurea*, the resulting hybrid has a tip, but much weaker than that present in *S. flava*.

In the matter of coloring, the blending is beautifully shown. If a form with red markings be combined with a green form showing no such markings, the hybrid will have the markings reproduced at half the intensity of the parent.

The flowers, in the matter of their size and shape, show a marked blending, though here too the hybrid is inclined to be larger and more showy than either parent.

A remarkable series is shown in the comparative petal shape and size. The figures given show how intermediate the hybrid is in relation.

In odor also the hybrid blends the parental characters—for instance, *S. flava* has a very decided and unpleasant odor, while *S. Drummondii* has a rather delicate sweet scent. Their hybrid has a stronger odor than *S. Drummondii*, but not at all unpleasant.

The intermediate relation in the matter of flower coloring in the three sets has been noted. Quite noticeable is the peculiar maroon color obtained in the hybrids with *S. Drummondii* as a parent.

All of these examples of blending parental characters seen in the hybrids are such as any one can note with the naked eye. The intermediate relation is, however, much more intimate and

exact. It extends to microscopic details in structure to be noted below.

The epidermal cells of the outer surface of the pitcher and of the inner lid surface show a blended appearance in the hybrid. Take for example *S. Moorei* (fig. 12), whose cells are intermediate between the rounded epidermal cells of *S. Drummondii* (fig. 11) with their pronounced papillation; and the wavy walled cells, without papillae, of *S. flava* (fig. 9).

The epidermal cells of the conducting surface of the hybrids are remarkably intermediate between the parents. Here there are measurable differences in length of cell and tip of process, and it has been shown that the hybrid lies exactly between the parents in length relation, breadth, and tip length.

On the outer and inner surfaces where stomata are present, the hybrid shows the number present in a given field to be an exact arithmetical mean between the numbers present in the parents. In regard to their distribution it has been noted that in other species the stomata are equally distributed over the surface, while in *S. Drummondii* they are limited to special tracts between the window areas. The hybrids with *S. Drummondii* show the stomata distributed in wide tracts (figs. 12, 14).

The unicellular hairs distributed over the various surfaces show several interesting relations.

On the detentive surface, the hybrid presents an arithmetical mean between the parent types in number and length of hair in each set. Over the outer surface of the pitcher, where the hairs are irregularly scattered, the relation is somewhat obscured. But in *S. flava* (fig. 9), *S. Catesbaei* (fig. 10), *S. purpurea* (fig. 8) one may see how the hybrid shows a variety of hair lengths inherited, and an intermediate degree of blending in the hairs.

On the inner lid surface, the hairs of all except two species show great variability in length. The hybrids with either of these two forms *S. flava* and *S. Sledgei* as a parent, having fairly uniform hairs, with any of the other forms, having variable lengths, show hairs of all lengths reproduced, but fewer in number and with the longest hairs much reduced.

This behavior of hair-length inheritance has been noted before in other plants (29) so that this seems to be a rule of inheritance for hair length and number.

In relation to the actual structure of the pitcher, longitudinal sections of the rim have been compared. It has been noted that, in the rolling, in the shape of the tip, in the amount of thickening at the tip, the hybrid is intermediate in character.

In all transverse and longitudinal sections of the pitcher, the number of layers of false palisade, of subepidermal cells, and the depth and character of the mesophyll, have all indicated an intermediate relation in the hybrid.

In the amount of thickening, either in sclerenchymatous tissue about bundles, or in the number of striations on the hairs of the inner lid surface, the hybrid is invariably intermediate.

Bisexual Hybridity

Some apparent variations from the exact blending should be noted here. On pages 16 and 17 there is an account of the inability of the glandular surface of *S. purpurea* to blend with the conducting surface of *S. flava*. The resulting mosaic effect is described. This obtains also in the hybrid of *S. purpurea* with *S. Drummondii*, and has been noted in the hybrid with *S. minor*. The inability is probably due to the fact that *S. purpurea* has evolved far in advance of all other forms, except possibly *S. Sledgei*. It would be interesting to know if of all the forms this could perfectly blend with *S. purpurea* when crossed. Unfortunately such a hybrid has not been found.

In the hybrid of *S. Sledgei* with *S. Drummondii*, the developing glandular area is completely lacking; the impulse is too weak for transmission.

Other peculiarities of relation in parent and hybrid types might be illustrated by the relation shown in comparisons of counts obtained for glands. In every case practically the hybrid shows fewer glands than either parent. It is almost impossible to obtain a hundred or more counts from a given surface, and compare it with a hundred similar counts from exactly corresponding surfaces. The glands are grouped in *S. flava* for instance around the rim, and down the median back portion of the pitcher. They extend halfway down the length. In *S. Drummondii* they are massed about the rim too, but are very sparse just below. If the total number of glands could be counted and compared, they would undoubt-

edly show a perfectly exact relation. This is upheld by the fact that where a surface without glands (in *S. flava*) is crossed with a surface where the gland number is uniform (glandular of *S. purpurea*) the hybrid shows an exactly intermediate number. In the case too where they are massed in the same regions in parents and hybrids, as in *S. Sledgei*, *S. Drummondii*, and *S. areolata*, the hybrid shows a blended relation.

The comparison of these three hybrid plants with their parents in all details of structure gives an overwhelming mass of evidence for exact blending, which extends to the most minute details. It surely points to some exact relation in molecular structure of the hybrid plant, extending even to the amount of thickening laid down in a cell wall, the size of the starch grains, or the size of a chloroplast.

The writer wishes to acknowledge the kindness and cooperation of Dr. J. M. Macfarlane in the preparation of this paper. Thanks also are due to Mr. W. R. Taylor, who made many of the microphotographs; and, through the kindness of Mr. Frank M. Jones, the writer was able to examine fresh flowers, which he sent from Alabama, Mississippi, and Florida.

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EXPLANATION OF PLATES

PLATE I.
Fig. 1. *S. purpurea.*
Fig. 2. *S. flava.*
Fig. 3. *S. Catesbaei.*
Fig. 4. *S. Drummondii.*

PLATE II.
Fig. 5. *S. Moorei.*
Fig. 6. *S. Sledgei.*
Fig. 7. *S. areolata.*

(The above photographs were made by W. R. Taylor from specimens in the Sarracenia House at the Univ. of Penna. Bot. Gardens.)

PLATE III. Micro-photographs of outer epidermis of lids of pitchers × 70.
Fig. 8. *S. purpurea.*
Fig. 9. *S. flava.*
Fig. 10. *S. Catesbaei.*
Fig. 11. *S. Drummondii.*

Fig. 12. *S. Moorei.*
Fig 13. *S. Sledgei.*
Fig. 14. *S. areolata.*

PLATE IV. Micro-photographs of the inner epidermis of lids of pitchers × 50.
Fig. 15. *S. purpurea.*
Fig. 16. *S. flava.*
Fig. 17. *S. Catesbaei.*
Fig. 18. *S. Drummondii.*
Fig. 19. *S. Moorei.*
Fig. 20. *S. Sledgei.*
Fig. 21. *S. areolata.*

(Photographs by W. R. Taylor.)

PLATE V. Micro-photographs of epidermal cells of the conducting surface × 500.

Fig. 22. *S. purpurea.*
Fig. 23. *S. flava.*
Fig. 24. *S. Catesbaei.*
Fig. 25. *S. Drummondii.*
Fig. 26. *S. Moorei.*
Fig. 27. *S. Sledgei.*
Fig. 28. *S. areolata.*

(Photographs by W. R. Taylor.)

A Comparative Study of the Structure and Saprophytism of the Pyrolaceae and Monotropaceae with Reference to their Derivation from the Ericaceae

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[Thesis presented to the Faculty of the Graduate School in partial fulfillment of the Requirements for the Degree of Doctor of Philosophy.]

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Introduction

In the families of flowering plants which show saprophytism and parasitism there occur usually green purely autophytic plants with typical green leaves and numerous flowers; plants that are purely saprophytic or parasitic, with colorless scales and a reduced number of flowers; and all gradations between. In a comparative study of such typical families showing saprophytism, *i.e.*, the Burmanniaceae, Orchidaceae, Gentianaceae, and Ericaceae, and those showing parasitism, the Loranthaceae, Santalaceae, Balanophoraceae, Rafflesiaceae, Lauraceae, Convolvulaceae, and Scrophulariaceae, one notices a common tendency in the saprophytic or parasitic members toward condensation and simplification as the saprophytism or parasitism becomes more pronounced. To illustrate from the parasitic group, in the Loranthaceae the genera *Nuytsia* and *Gaiadendron* are upright independent trees; the genus *Loranthus* consists of upright shrubs with large leaves and numerous flowers as *L. Baroni* Baker and *L. pulcher* D.C., to those with small leaves and solitary flowers as *L. microcuspis* Baker and *L. stocksii* Hook.; *Viscum* consists mainly of species of condensed habit, small leaves often reduced to scales, and small green unattractive flowers and more or less simplified embryos; finally *Arceuthobium* consists of reduced almost leafless parasites becoming slightly yellowish in color with small solitary flowers. In this family, however, the plants still contain chlorophyll. In the Convolvulaceae the parasitism has become so great in the genus *Cuscuta* that it has completely lost all traces of chlorophyll, except in the stems of *C. reflexa*, Roxb. (Hooker in Bot. Mag. t. 6566). From this species we have gradations to others with thick yellow stems like *C. exaltata*, Engelm.; others with slender yellowish or red stems as *C. epilinum* Weihe and *C. epithymum* Murr, pale yellow in *C. arvensis* Beyrich, and whitish or pale yellow in *C. cephalanthi* Engelm., and finally to white in *C. epithymum* var. *alba*. The leaves are in all cases reduced to microscopic scales; the flowers are small but clustered together; the first or central flowers are five-parted, the lateral ones often four-parted (15), and the embryo is so reduced that it shows no trace of cotyledons.

The writer, however, is concerned with saprophytism alone. In the Burmanniaceae, for example, the genus *Burmannia* shows transitions from green leafy plants with several racemose flowers as *B. longifolia* Becc. to gradually condensing forms, as *B. azurea* Griff. with a rosette of tiny herbaceous membranous leaves and one to four flowers, then to more simplified forms, as *B. tuberosa* and *B. candida*, and finally, most simplified of all, to the genera *Thismia* and *Gymnosiphon*. The stems become feeble, less green, then reddish or brownish. The green leaves become reduced to herbaceous membranous leaves, then to scales; the flowers become reduced in number and size; the ovary becomes reduced from a three-celled condition with central placenta to a more primitive one-celled state with parietal placentas (*Gymnosiphon*); there is an increase in the number of ovules, but a reduction in their size; the seeds are reduced in size and structure; the reserve albumen is reduced in size and number of cells, and the embryo from a typical monocotyledonous one to a formless mass.

The writer would claim that essentially the same set of changes can be traced in genera of the Orchidaceae and Gentianaceae. Green autophytes, passing by gradual changes to colorless saprophytes, occur in both of these. Now, among systematists of the past, there has been no thought of putting the saprophytic plants of the above three groups in separate families. Why then, it may be asked, should the Pyrolaceae and Monotropaceae be separated from the Ericaceae? It will be the writer's aim in the present paper to prove, alike on morphological and physiological, as well as taxonomic grounds, that these three families all show so close a relationship that to view them as separate families is unnatural and artificial.

Jussieu (37) considers all ericaceous plants under the two orders—Rhododendra and Ericae—the latter including Pyrola. Lindley (46) places them in three orders—Ericeae, Vaccinieae, and Pyrolaceae (including Monotropaceae). De Candolle (10) makes four orders—Vaccinieae, Ericaceae, Pyrolaceae, and Monotropeae. Gray (25) considers the Vaccinieae, Ericineae, Pyroleae, and Monotropeae as suborders of the Ericaceae. Baillon (3) considers the Pyroleae, Monotropeae, and Pterosporeae as three of the eighteen tribes under the Ericaceae. Bentham and Hooker (4) make three orders, the Vacciniaceae,

Ericaceae (including as a tribe the Pyroleae), and the Monotropeae. Drude (12) gives two families—the Ericaceae and the Pyrolaceae (including the Monotropaceae). Britton and Brown (6) consider as separate families the Pyrolaceae, Monotropaceae, Ericaceae, and Vacciniaceae. Small (72) considers the Pyrolaceae, Monotropaceae, and Ericaceae as distinct families. So we see that the Pyrolaceae and Monotropaceae are united by the majority of systematists, yet the gulf between the two is really more difficult to bridge than that between the Ericaceae and Pyrolaceae.

Drude in "Die Natürlichen Pflanzenfamilien" (12) gives as his reasons for not including the Pyrolaceae and the Monotropaceae in the Ericaceae: (1) the remarkable placentation, (2) the regular form of the seed and embryo in the Ericaceae, (3) the lacking disc, (4) the dehiscence of the anthers, (5) the simple pollen of the Monotropeae.

(1) In typical Ericaceae the ovary is five- or four-celled with a central placenta. Two lobes bearing the ovules extend into each cell of the ovary. It is generally considered to be five-celled in the Pyrolaceae also, but the division is not complete. The parietal placentae borne in on the dividing walls fuse at the center for about half the length of the ovary. This basal half is exactly similar to that of the Ericaceae, two placental lobes bearing ovules extending into each cell. Above this the placentae fail to meet at the center and the upper half becomes one-celled with bilobed parietal placentae. This condition is true of *C. umbellata*, *C. maculata*, *P. rotundifolia* (*P. americana* Sweet), *P. elliptica*, *P. secunda*,* *P. minor*, *P. chlorantha*, *P. aphylla*, *Moneses uniflora** of the Pyrolaceae; also of *Allotropa virgata*, *Pterospora andromedea*, *Sarcodes sanguinea*, *Schweinitzia odorata*, *Monotropa hypopitys*, *M. uniflora*, of the Monotropaceae. The division Pleuricosporeae of the Monotropaceae is considered one-celled in the ovary. *Newberrya* is described by Torrey in the Ann. Lyc. N. Y. VII 55 (1864): "Placentae four with broad divergent lamellae which meet adjacent edges, ovuliferous both sides giving the appearance of

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* *P. secunda* and *Moneses uniflora* are almost completely five-celled. Owing to the sunken style the distance through which the ovary is one-celled is very short.

four exterior cells surrounding a central large one." The writer examined material of *Newberrya spicata* A. Gray and *N. congesta* (A. Gray) Torr. and found an exactly similar condition to that in the rest of the family—*i.e.*, that the ovary at the base is five-celled owing to the fusion of the placentae and that owing to a lack of fusion further up the ovary became one-celled with parietal placentae. *Pleuricospora fimbriolata* A. Gray shows the most simplified condition in regard to the ovary. It is four-celled only at the very base for about one-sixth the distance, then one-celled with four parietal placentae.

(2) In typical Ericaceae the seed is very small, never larger than 1–2 mm. The seed covering is double, there is a richly developed endosperm in which is embedded a straight embryo which is one-third to two-thirds the length of the seed. The embryo always shows a root, an axis, and two cotyledons. The seeds in the Rhododendroideae-Ledeae, the tribe nearest in character to the Pyrolaceae, are winged, very small, and contain a very small embryo. These seeds are very similar to those of the Pyrolaceae, except that in the latter the embryo itself is very much smaller, simplified to a few cells, and with no differentiation into root or cotyledons. The amount of albumen in which the embryo is embedded is also reduced.

(3) There is in practically all typical Ericaceae, at the base of the ovary, a nectar-secreting disc which may be present as a circular ring or a crenulately lobed swelling. Müller has illustrated those of *Arctostaphylos*, *Calluna*, *Erica*, *Azalea*, *Rhododendron*, and Warming those of *Andromeda*, *Cassiope*, *Phyllodoce*, in Knuth's "Handbook of Flower Pollination" (42). Drude (12) seems to indicate that it is lacking in the Pyrolaceae and Monotropaceae and gives this as a reason for separating them from the Ericaceae. In *C. umbellata* and *C. maculata* it is present as a nectar-secreting ring at the base of the ovary. In the genus *Pyrola* the disc varies. According to Drude (12) it is present as a ten-rayed nectar-secreting organ in *P.* (*Moneses*) *uniflora*, but Müller (42) states that there is no nectar secreted by *M. uniflora* and figures no nectaries. The writer sees no trace of nectaries in the material examined. Drude states that the disc is present as ten small nectaries at the base of the ovary in *P. secunda* and is absent or rudimentary in all of the other species. The writer found very small swellings that

appeared glandular at the base of the ovary in *P. secunda*, *P. chlorantha*, *P. aphylla*, but none in *P. rotundifolia*, *P. elliptica*, and *P. minor*.

In the Monotropaceae Drude says "Disc present, or replaced by nectaries, rarely lacking." In *Allotropa*, according to Torrey and Gray (77), it is minutely ten-lobed. The writer finds ten slightly downward directed lobes; in *Monotropa* there are 8–10 downward directed nectaries; in *Sarcodes** there are ten swellings at the base of the ovary; in *Pterospora* Drude reports that it is absent.

In *Schweinitzia* there are ten lobes between the stamens. Drude states that in the Pleuricosporeae the disc is entirely lacking in *Newberrya*, *Pleuricospora*, and *Cheilotheca*. This appears to be true of *Pleuricospora* but in *Newberrya* the writer finds that ten nectaries are present at the base of the ovary, very similar to those of *Monotropa*. No material of *Cheilotheca* could be obtained for examination.

(4) In the Pyrolaceae and Monotropaceae the dehiscence of the anthers follows one of these types.

1. Apical porous—with more or less developed tubes in *Chimaphila*, *Pyrola*, *Moneses*, *Sarcodes*, *Schweinitzia*.
2. Longitudinal—*Allotropa*, *Pterospora*, *Pleuricospora*, *Newberrya*, *Cheilotheca*.
3. Transverse—*Monotropa*.

In the Ericaceae apical porous and longitudinal dehiscence seem to be about equally distributed throughout the family and even in the same group, *i.e.*, in the Rhododendroideae-Ledeae *Bejaria* and *Ledum* have apical porous, *Elliottia* and *Cladothamnus* longitudinal dehiscence of the anthers. Transverse dehiscence of the anthers also occurs in the Ericaceae. The group Arbutoideae-Andromedeae, according to Drude (12), has pores or slits at the apex or transverse slits.

(5) The Pyrolaceae and Ericaceae have tetrad pollen grains, the Monotropaceae simple pollen grains. However *Pyrola secunda*, a typical member of the genus, has simple pollen grains so that even this distinction does not entirely hold true.

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* Drude reports no disc in *Sarcodes;* Oliver (58) that the disc is present. The writer's material confirms the latter.

We see, therefore, how artificial, untrustworthy, and interblending these distinctions are. There are also other great resemblances between the Ericaceae and the Pyrolaceae and Monotropaceae. All of the Ericaceae are shrubby rarely arborescent, often sub-shrubby. The Pyrolaceae as a whole are sub-shrubby, *Chimaphila umbellata* often becoming very thick, woody; most of the genus *Pyrola* is sub-shrubby also, with the exception of *Pyrola* or *Moneses uniflora*. The Monotropaceae are essentially saprophytic herbs, but they perennate from underground woody parts.

Historical

Owing to the complete historical references on the subject of mycorhiza in general given by Gallaud (22) and Rayner (64), the writer has confined herself to those dealing with mycorhiza in the Ericaceae alone.

As early as 1842, Rylands (67) investigated the "byssoid" substance on the roots of *Monotropa hypopitys* and came to the conclusion that it was a fungus living on the roots. In 1856–1865, Chatin (6) described *M. hypopitys* as a parasitic plant. In 1873, Drude (11) investigated the roots of *M. hypopitys*, coming to the conclusion that the plant is saprophytic. In 1881, Kamienski (38, 39) also described and figured the condition in *M. hypopitys*, and formulated the hypothesis that there existed a symbiosis between the plant and the fungus. During the last thirty-five years, it has been shown that saprophytism is widespread throughout the Ericaceae proper. Frank (19), in 1887, described the appearance of ericaceous roots infected by fungi. He mentions particularly the much enlarged epidermal cells, filled with knots of hyphae, the absence of root hairs, and the reduction of the root cap. Those mentioned as possessing endotrophic mycorhiza are *Andromeda polifolia*, *Vaccinium oxycoccus*, *V. uliginosum*, *V. macrocarpum*, *V. myrtillus*, *V. vitis-idaea*, *Ledum palustre*, *Calluna vulgaris*, *Rhododendron ponticum*, *Azalea indica*, *Empetrum* (included by him under Ericaceae). He says, however, that they have not been found in *Pyrola* and that in *Monotropa* the mycorhiza is ectotrophic.

In 1907, Charlotte Ternetz (77), in a paper "Ueber die Assimilation des Atmosphärisches Stickstoffes durch Pilze," used as the basis for her experiments endotrophic fungi in the roots of *Andromeda polifolia*, *Oxycoccus palustris*, *Calluna vulgaris*, *Erica carnea*, *E. tetralix*, *Vaccinium myrtillus*, *V. vitis-idaea*, *V. uliginosum*. She states that, although hyphae are present in the seed coats, no trace of the fungus can be found in any other living part of the plant, except the roots. Rayner (63) in an article on "Obligate Symbiosis in *Calluna vulgaris*" traces the fungus from the roots through the whole plant to the seed. She proves that the symbiosis in *Calluna* is obligate, for, unless the seedlings become infected, they die. She also states that ovarial infection is present in *Ledum palustre*, *Rhododendron ponticum* (garden var.), *Rhododendron indicum* (*Azalea indica*, garden var.), *Leiophyllum buxifolium*, *Kalmia angustifolia*, *Pieris floribunda*, *P. japonica*, *Gaultheria acutifolia*, *Arctostaphylos uva-ursi*, *Arbutus unedo*, *Vaccinium vitis-idaea*, *Pentaptergyium serpens*, *Calluna vulgaris*, *Erica carnea*. Jean Dufrenoy (14) in "The Endotrophic Mycorhiza of Ericaceae" has reported the presence of a fungal mycelium throughout the entire plant of *Arbutus unedo*.

All these cited are, however, still green, and have abundant leafy branches with well-formed clusters of typically ericaceous flowers. It seems that the more simplified greens and the yellow and white saprophytic forms have been separated from the Ericaceae to form the Pyrolaceae and Monotropaceae, and that these three families in the order named form a continuous series from autophytic to completely saprophytic plants.

An aim of this paper will be to ascertain how far saprophytism has caused gradual and traceable degradation changes similar to those of the Burmanniaceae, Orchidaceae, and Gentianaceae. Practically all typical ericaceous plants are shrubs, rarely trees; some like *Cassiope* are sub-shrubby; in the Pyrolaceae *Chimaphila* and the larger species of *Pyrola* are sub-shrubby; but *Moneses uniflora* would hardly be regarded as other than a herb; in the Monotropaceae all of the genera are herbaceous. Another aim will be to find characters which unite the most degraded saprophytes with the autotrophic Ericaceae, thereby proving that the separation of the Pyrolaceae and Monotropaceae from the Ericaceae is artificial.

Methods and Materials Used

In making comparisons, care was taken to section the material at exactly the corresponding point in each of the plants.

Sections of freshly gathered or of alcoholic material of rhizomes, stems, and leaves were examined unstained in acetic acid, or stained in safranin and methyl green and examined in balsam.

Fresh root tips were examined in a solution of iodine in potassium iodide to differentiate the fungus. Otherwise, all roots and flowers were fixed in weak chrom-acetic acid and embedded in paraffin. These were stained in safranin and gentian violet.

Pieces of the ascending axis of *Monotropa uniflora* and *M. hypopitys* were bleached and macerated in a mixture of 50% nitric acid and potassium nitrate in order to examine the epidermis.

Herbarium material of the flowers was prepared for examination by the method used by R. C. McLean (52).

The following is a list of the plants used, and localities from which they were collected, for use in this comparison:

Fresh Material

Chimaphila umbellata—Hosensack, Pa., Analomink, Monroe Co., Pa., Somers Point, N. J., Glendora, N. J., Woods Hole, Mass., Greenwood Lake, N. Y.

Chimaphila maculata—Hosensack, Pa., Crum Creek, Delaware Co., Pa., Almonessen, N. J., Blackwood, N. J., Somers Point, N. J., Woods Hole, Mass.

Pyrola rotundifolia—Hosensack, Pa., Crum Creek, Delaware Co., Pa., Analomink, Monroe Co., Pa., Woods Hole, Mass.

Pyrola elliptica—Hosensack, Pa., Crum Creek, Delaware Co., Pa., Analomink and Paradise Valley, Monroe Co., Pa., Woods Hole, Mass.

Moneses uniflora—Plants collected by Miss Mary Garley near Claremont, N. H.

Monotropa hypopitys—Analomink, Pa., Somers Point, N. J., Woods Hole, Mass.

Monotropa uniflora—Analomink, Pa., Blackwood, N. J., Woods Hole, Mass.

Kalmia latifolia, Kalmia angustifolia, Dendrium buxifolum, Cassandra calyculata—Clementon, N. J.

Ledum groenlandicum—Peakes Island, Maine, collected by Miss A. M. Russell.

Alcoholic Material

Sarcodes sanguinea—Collected by Miss Edith M. Farr in California.

Herbarium Material

Descriptions of the plants and microscopic studies of the flowers of *Pyrola secunda*, *P. minor*, *P. chlorantha*, *P. aphylla*, *Pterospora andromedea*, *Schweinitzia odorata*, *Pleuricospora fimbriolata*, have been made from the Herbarium of the University of Pennsylvania. Those of *Allotropa virgata*, *Newberrya spicata*, *N. congesta*, were examined from the Herbarium of the Philadelphia Academy of Natural Sciences.

As it was impossible for the writer to get fresh material of the roots of *Moneses uniflora*, the Herbarium of the Bronx Botanical Garden, through the kindness of Dr. F. W. Pennell, sent several herbarium sheets for examination.

Through the kindness of Mr. W. R. Taylor, the writer was given the opportunity of examining sections of the leaves and stems of ericaceous plants, collected on Mount Washington by him, including *Cassiope hypnoides*, *Chiogenes hispidula*, *Ledum groenlandicum*, *Loiseleuria procumbens*, *Rhododendron lapponicum*, *Vaccinium uliginosum*, *V. vitis-idaea*.

The writer wishes to state here her deep appreciation of the assistance given and the constant interest shown by Dr. J. M. Macfarlane in the preparation of this paper.

The Underground Root and Stem Systems

The mature underground system in *C. umbellata* consists of horizontal, thick, white runners or rhizomes bearing scales, in the axil of which occur two buds, the first developing into another branch or runner, the second into an adventitious root. The end of the runner finally pushes above the surface of the ground and produces a whorl of leaves. The roots are very small, wiry, and do not branch profusely. This method of underground stem branching is characteristic of a number of typical Ericaceae. Warming (84) describes and figures it for *Andromeda polifolia* L., *Vaccinium myrtillus* L., *V. uliginosum* L., *V. vitis-idaea* L., *V. oxycoccus* L. (figs. 19, 27, 29, 32, 35).

The underground systems of *C. maculata*, *Pyrola rotundifolia*, *P. elliptica*, *P. secunda*, *P. minor*, *P. chlorantha* are similar to that of *C. umbellata* (Warming (84) figs. 38, 39).

In *P. aphylla*, it consists, according to Holm (30) of runners as in the other Pyrolas, one of which rising to the surface may

produce green leaves, another an inflorescence with only scale leaves. Holm and Drude (12) report the presence of adventitious buds arising from the roots and forming flowering or vegetative shoots. Irmisch (30) reports this same reproduction by root shoots in *P. secunda* and *P. chlorantha*. Holm states that this also occurs in *P. picta*, *C. umbellata*, and *C. maculata*, though none of the writer's material of the latter genus shows this.

This reproduction by adventitious buds from the roots in *P. aphylla* forms a connecting link with the condition in *Moneses uniflora*. Warming (85) and Irmisch (32) state that in this species there is a horizontal root from which arises a leaf-bearing shoot terminating in an inflorescence. Warming states that a root arises from the horizontal one at the base of each shoot. In other words, there is no rhizome present; the horizontal root here takes over the function of the rhizome in producing leaf- and flower-bearing shoots. The occasional production of adventitious buds on the roots of *P. aphylla* has become habitual in *Moneses uniflora*—this being the only method of vegetative reproduction in the latter. The main root of *M. uniflora* resembles the rhizomes in the Pyrolas excepting for the absence of scales on it; normal secondary roots are produced from the root at the base of the vegetative shoot and at irregular intervals along its course.

MacDougal (48) states that "*Pterospora andromedea* is furnished with an ovoid mass of dark brown club-shaped roots which ramify densely through a space of not more than 150–200 cc. in which the roots occupy a much greater proportion of the volume than the included humus." There are several primary roots which branch and rebranch, all intertwining to form a "compact globoid mass." He states that inflorescence buds arise from the horizontal root.

Oliver (58) has described the appearance of the root system of *Sarcodes sanguinea*. He states: "The roots are attached in great quantities to the bases of the flowering shoots and form large and intricately woven masses of 'coralline' appearance." The main axis bears numerous secondary roots which in turn produce tertiary ones. The surface is of a "deep brown color," showing a "certain roughness of texture" due to their being invested with a fungal sheath. He states that the plant is vegetatively reproduced by buds from the roots.

In *Monotropa* there is a similar mass of roots. The main root is thick, horizontal, giving rise to inflorescence buds and to secondary roots, which are short, fleshy, and intertwine closely to form a compact mass. Drude (11), Kamienski (39), Queva (62) call this horizontal structure a root. Peklo (59) calls it a "Rhizomäste." The structure is so simplified that it is difficult to determine whether it is a root or a rhizome.

There is therefore in the underground root and stem system a gradual condensation and simplification from genera like *Chimaphila* and *Pyrola*, which have, as in certain typical Ericaceae, extensively branching rhizomes from which are produced the vegetative axes as branches in the axils of scales, to *Moneses*, where the rhizome is completely lacking and the vegetative axes arise endogenously from an old horizontal root which closely resembles a rhizome in appearance; to *Pterospora*, *Sarcodes*, and *Monotropa*, where the horizontal root has become very much condensed, thickened, and fleshy, also producing vegetative buds endogenously. The roots, from being thin, wiry, and sparsely branching in *Chimaphila* and *Pyrola*, have the primary root enlarged and thickened in *Moneses*, *Pterospora*, *Sarcodes*, and *Monotropa*. The secondary roots begin to show a slight swelling at the tip in *P. rotundifolia* and *P. elliptica*. This swelling becomes greater, secondary roots become shortened, thickened, and more fleshy and much more numerous, so that there is a close compact mass of roots in *Pterospora*, *Sarcodes*, and *Monotropa*.

The Root

In *Chimaphila umbellata*, sections of the root tip (fig. 1, 1) show a short root cap of 4–5 layers at the very tip. This together with the epidermis arises from a common tissue, there being only three regions of growth, the calyptro-dermatogen, the periblem, and the plerome. The epidermal cells at the tip are small, indistinguishable in size from the others, but soon show gradual increase in size, particularly in a radial direction—the radial width becoming three to four times the length. This gradual increase occurs under the root cap, this region never being infested by fungi. Above the root cap, the cells suddenly become larger and square in section. These cells are infested

by septate hyphae which appear as balled-together masses in the epidermal cells. All cells and all roots are not equally infested—some roots show no trace of hyphae; others show a few epidermal cells with two or three hyphal threads; others show some epidermal cells packed full of masses of hyphae and a hypertrophied nucleus, and cells in the same root with normal nucleus and cytoplasm. Rommel (65) states that there are no hyphae present in the roots of *C. umbellata* and that root hairs are present. The writer has examined material from many localities, and has found some roots of each plant infested with hyphae and has never found any traces of root hairs. Beneath the epidermis are one to two layers of elongated cortical cells crowded with typical aggregate starch grains composed of two to six simple grains, each with a distinct hilum. These appear in safranin-stained sections as hyaline grains with red staining hila. In the same or neighboring cells these grains appear slightly yellowish, but still with a distinct hilum, then yellowish brown with no hilum apparent; and finally the individual grains merge together to form a sac of brownish material. The secondary roots are produced endogenously.

The root tip of *C. maculata* has much the same appearance as that of *C. umbellata*, except that the epidermal cells of the former beneath the root cap are longer compared with their radial width; these above the root cap are larger in comparison with the other cells than are those in *C. umbellata*, are more often, and, to a greater extent, infested with hyphae (Fig. 2, 1); and also in those cells not filled with hyphae there appear one to three large bladders, the walls of which are light yellowish in color. These may be the remains of the nuclear membrane after the nucleus has been completely destroyed by the fungus, or enlargements formed by the hyphae similar to those described by Groom (28) in the mediocortex of the absorbing organ of *Thismia aseroë* and by Gallaud (22) in the roots of *Colchicum autumnale*. The writer however did not find any hyphae attached to these bladders.

In *Pyrola rotundifolia* (Fig. 1, 2) the root cap is strongly reduced, there being only one to two layers of cells. The aspect of the cells at the tip, under the root cap region, is much the same as in the two species just described; but above the root cap the epidermal cells swell out enormously, much more than

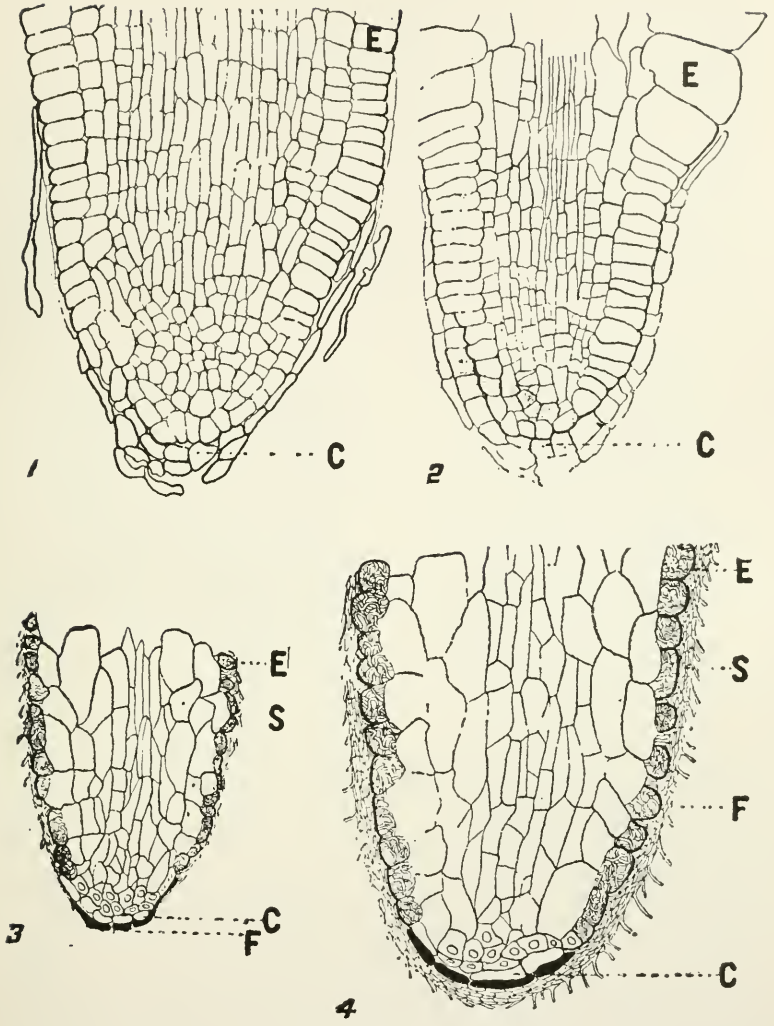

Fig. 1. Longitudinal sections (×250) of root-tips of
1. *Chimaphila umbellata*
2. *Pyrola rotundifolia*
3. *Monotropa hypopitys*
4. *Monotropa uniflora*

C = root cap, E = epidermis, F = free hyphal filaments, S = hyphal sheath.

in *C. umbellata*, or *C. maculata*, and practically every cell becomes filled with balled-together masses of hyphae. There also occurs on the outside of the epidermis a network of intertwining hyphae (Fig. 2, 2), forming a sheath *S* from which extend separate filaments *F* which apparently take the place of root hairs in supplying the root with water. There is a connection between these outer hyphae and those in the epidermal cells. These hyphae grow between and around the epidermal cells, until they surround them on all sides, except the interior; so that a tangential section shows epidermal cells

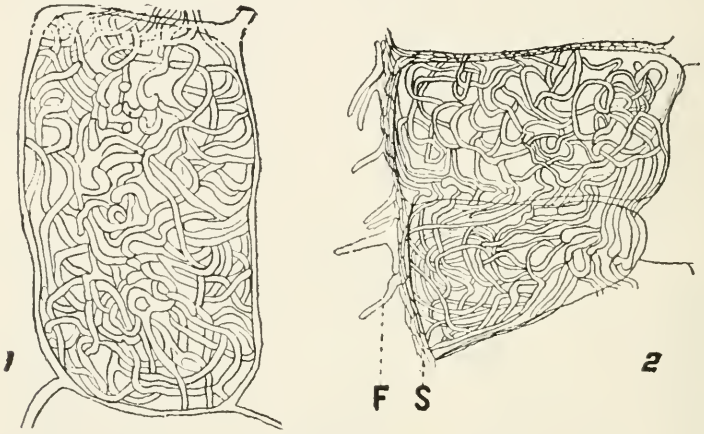

Fig. 2. Longitudinal sections (×300) of epidermal cells of root tip.
1. *C. maculata*
2. *P. rotundifolia*
F = free hyphal filaments, S = sheath.

separated by a pseudoparenchyma, much like that seen in *Monotropa*. There is apparently no invasion of any layer beneath the epidermis. Kramar (44) has described all stages of the growth of the mycorhiza. The walls of the epidermal cells first become infested with hyphae forming a pseudoparenchyma between the cells. Later, when the epidermal cells become full size the hyphae penetrate the cell wall, make direct for the nucleus and begin to form a ball around it. The nucleus finally becomes hypertrophied and lifeless. When this occurs and the cell is packed full of hyphae they penetrate the cell wall again and spread out over the surface. Before this occurs

Kramar says that the fungus is only a parasite drawing its nourishment from the plant. After the outer covering is formed, however, the fungus can then take the place of root hairs and absorb water for the plant. It may also give a part of its own assimilated food to the plant. Frank observes that as the fungus dies each year the plant could then absorb its protein content. Kramar also describes the contents of the subepidermal cells, that they are coarsely granular and that these cells represent a storage place where the nutritive material, taken in by the mycelium, lies until ready to be transferred to where it is to be used. He probably saw the starch grains similar in appearance to those of *Chimaphila* when they had become disintegrated to the extent of not showing a hilum.

Pyrola elliptica has practically the same appearance as *P. rotundifolia*. *P. secunda* is reported to have fungal hyphae by Irmisch (32), Rommel (65), Andres (2), Petersen (60); *P. minor* by Kramar (44) and Petersen (60).

P. aphylla is described by Holm (30) as having the root free from hyphae. This seems rather improbable in view of the fact that all the other members of the genus have been reported to have hyphae in the roots. The writer has not been able to get fresh material of this for examination.

Moneses uniflora is reported by Irmisch (32) to have fungal hyphae in the roots.

In *Monotropa hypopitys* (Fig. 1, 3) Kamienski (39) and Drude (11) describe the root tip as having one to two layers of root cap, Drude claiming that in one variety—*hirsuta*—there are two layers, and in *glabra* only one. Kamienski, however, says that the number of layers may vary in the same individual. The material examined shows one to two layers of root cap, the outer layer crushed and flattened. All the cells at the tip are very much alike, differentiation into plerome and periblem occurring some distance back from the tip. Kamienski (39) and Peklo (59) have given complete descriptions and accurate figures of the root tip of *M. hypopitys*. In the *Chimaphila* and *Pyrola* species described the fungus does not seem to invade the root cap region either in the root cap itself, over its surface, or in the epidermal cells beneath. In *M. hypopitys*, though the epidermal cells under the root cap and the root cap cells are not infested, the mycelium extends over the surface of the root

cap—though thinner here than over the rest of the root. As in *P. rotundifolia* there is a development of pseudoparenchyma between the epidermal cells and a continuation of this on the exterior forming a sheath much greater in thickness than in *P. rotundifolia*. This outer sheath consists of two regions, the inner composed of closely intertwined hyphae, the outer of more loosely arranged threads that stray out into the soil. Kamienski claims that the hyphae never penetrate the epidermal cells, but that sometimes in older parts a hypha may penetrate an epidermal cell, which it fills with a brown content. He also says that over the apex the sheath thins out so that there are only several isolated filaments. MacDougal and Lloyd (50) state that the hyphae do penetrate the epidermal cells, forming swollen vesicles, and that the root tip is completely invested by a thin fungal sheath. Peklo figures the penetration of haustoria into the epidermal cells. He states that haustoria are present in all infested roots of this species. The hyphae do not completely fill the cell as in *P. rotundifolia* because there is present a vacuole of yellowish brown substance. Drude calls this a pigment; Kamienski notes its presence in dead cells only, and states that it is tannin; Bokorny (5) that it is tannin in the living cells. The latter, noting that there seems to be no difference in the quantity of this material from the youngest to the oldest epidermal cells, concludes that it cannot have anything to do with the nutrition of the fungus but that it serves, on account of its strongly concentrated tannin content, as a protection against the hyphae. Peklo also notes that beside this the resistant cuticle of the layer beneath keeps the fungus from penetrating further into the root. He claims that there are two ecological varieties of *M. hypopitys*, one living in humus, with the roots near the surface; the other in loamy soil, the roots deep underground. In the former, he says that hyphae are always present and indispensable to the life of the plant; in the latter, there are no mycorhiza in a great majority of the roots. The writer's material, however, was collected in a loamy soil with a surface covering of humus, the roots about 5 dm. below the surface, and all were strongly infested with hyphae. One difference between the epidermal cells of this species and those of *P. rotundifolia* is that they are not enormously enlarged in comparison with the rest of the

cells—in fact the epidermal cells in *M. hypopitys* are smaller than those of the layer beneath. MacDougal and Lloyd (50) report the presence of starch in the cortex of the roots of *Monotropa* near the tip, though the material examined by the writer failed to show this. According to Kamienski, secondary roots arise endogenously as in the Pyrolaceae.

The root tip of *M. uniflora* (Fig. 1, 4) is quite similar to that of *M. hypopitys*, except that at the apex the regions of growth are even less distinguishable; the pseudoparenchyma between the walls appears to be better developed; and the outer layer of the sheath formed by the intertwining hyphae does not thin out over the apex as in *M. hypopitys*, but continues as a layer of the same thickness completely around the root tip. This has been described and figured by MacDougal and Lloyd (50) (p. 10, Pl. 11). The root cap consists of one to three (MacDougal and Lloyd 1–4) layers of flattened cells filled with deeply staining material. The cells appeared crushed in all of the root tips examined. The area which the root cap covers is exceedingly limited. MacDougal and Lloyd have figured all stages of the penetration and development of the fungus in the epidermal cells. The nucleus becomes deformed; the hyphae form grape-like clusters, which they consider to be atrophied reproductive branches. They also state that starch grains occur in the outermost layer of the cortex and that secondary roots arise from the third layer of the cortex.

Oliver (58) has described and figured the root tip of *Sarcodes sanguinea* Torr. The appearance is very like that of *Monotropa uniflora*. In *Sarcodes* the root cap is better developed. Oliver figures five layers. The fungus surrounds each epidermal cell, and forms a sheath of hyphae on the surface. He states that the hyphae never penetrate the epidermal cells, but he also mentions that the nuclei of the epidermal cells are modified into rod-like structures. MacDougal and Lloyd mention the presence of the mantle of mycelium that extends completely around the root tip; that this is composed of two regions as in *Monotropa* and that the hyphae penetrate the epidermal cells. In the layer beneath the epidermis Oliver figures a few starch grains. He reports that secondary roots arise exogenously.

MacDougal (48) in "Symbiotic Saprophytism" and MacDougal and Lloyd (50) have described the root tip of *Ptero-*

spora. It is coated with a dense brownish septate mycelium which pushes in between the epidermal cells, penetrates them, forming irregular vesicles and distorted nuclei, and even enters the sub-epidermal layers. A root cap is present, and MacDougal states that this resembles that of *Sarcodes*, in having more than two layers. The mycelium covers the root cap and penetrates the older cells in free tips, but penetrates beneath the root cap in those roots that are in the center of the clump. He states that starch is present in the outer cortical layers and that secondary roots arise exogenously.

Thus in the root tip region we have a gradually ascending series in the amount of fungus present from *C. umbellata*, with the epidermal cells of some roots with no hyphae—other roots with hyphae, but not in every cell; to *C. maculata* with a still greater number of the epidermal cells filled with hyphae; to *P. rotundifolia* and *P. elliptica* with all of the cells infested and with a beginning of a sheath of intertwined hyphae around the root tip; then in *M. hypopitys* an increase in the width and extent of this sheath and a division of it into two zones—the outer a more loosely interwoven mass of hyphae, the inner more compact; finally in *M. uniflora* a still greater width of the fungal sheath. The descriptions of the presence of hyphae in *Sarcodes* and *Pterospora* show a great resemblance to *Monotropa*, but not having material to examine the writer cannot say which has the larger amount of mycelial investment. In *Chimaphila* the hyphae are probably not of much use to the plant as the threads are only in the epidermal cells and do not extend out over the surface. The development of an outer sheath of hyphae in *Pyrola* and its great increase in amount in *Monotropa*, *Sarcodes*, and *Pterospora* would allow the fungus to be of more use to the plant and that this is true is indicated by the lack of green coloring matter in the last three mentioned.

Sections both longitudinal and transverse of the oldest portion of the root were examined in all of the preceding. In *C. umbellata*, as the root becomes older, the hyphae penetrate more between and into the epidermal cells, completely filling them all. The nuclei become disintegrated, the walls thicker, the cells die and finally fall off. The outermost layer of the cortex may have some of its cells penetrated by the fungus,

but this is rare. The walls of the outer cells of the cortex also become thickened and these also fall off. Meantime the 4–5 arch bundle system has undergone secondary thickening. New xylem cells have developed so that there is formed a solid central cylinder of wood enclosed by a few layers of thin-walled phloem cells. These roots are perennial and annual rings of wood are laid down. The oldest one examined was found to have four years of growth. The largest part of the wood seems to be composed of pitted vessels with a few spiral ones.

C. maculata, *P. rotundifolia*, and *P. elliptica* showed practically the same appearance except that none of the material examined was old enough to have formed annual rings or to have had the epidermis entirely dead and sloughed off.

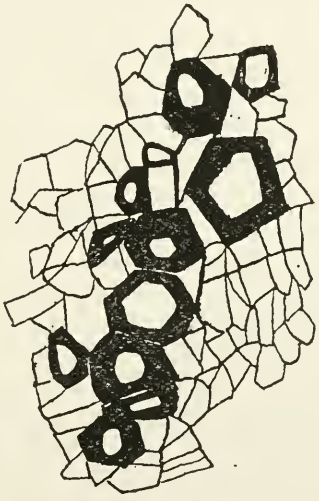

Fig. 3. Transverse section root of *Moneses uniflora* showing central xylem tissue × 300.

In *Moneses uniflora* the epidermal cells become filled with hyphae and fall off. Hyphae may penetrate into the outer layers of the cortex. The wood is at first diarch—a few remaining cells seem to indicate that this is a reduction from a tetrarch condition (Fig. 3). Secondary wood is formed.

MacDougal and Lloyd (50) have described the structure of the old root of *Sarcodes* and *Pterospora*. The epidermis becomes completely filled by the fungus and falls off. After this the

subepidermal cells divide radially to form a wider cortex. "The central cylinder of *Sarcodes* and *Pterospora* is least reduced and its development may be traced in them with some certainty. Here the 5–6 xylem bundles alternate with the simple phloem, enclosing a well marked medulla. The first step in the secondary growth is the sclerotization of the medulla, and is followed by the lignification of this tissue in *Sarcodes*. Next the phloem gives rise to a cambium which develops wood internally, and bast on the outside. The latter consists for the greater part of elongated elements of narrow lumen which do not undergo any marked thickening of the walls. The wood formed by the cambium joins directly on to the lignified medulla. The inner ends of the primary medullary rays also undergo sclerotization to some extent, but the outer portions show as broad bands one or two layers in thickness with the characteristic appearance of being compressed tangentially. The advance of the cambium is at first fairly regular, as the cambium zone moves outwardly beyond the first ring formed, the transformation into vessels is accomplished with such disturbance or variance from the customary manner that it is not possible to draw a line separating the two regions. Furthermore, some of the cambium cells of great size remain as great thin-walled elements in the wood, or these may be arranged in radial lines simulating tertiary rays. A region of cambiform elements, four to six layers in thickness, may be seen entirely surrounding the xylem. The structure formed by this behavior of the cambium resembles that of a stem, and indicates that the roots of the two genera in question may attain an age of two years or more."

In *Monotropa hypopitys*, the oldest part of the root is the horizontal portion that gives off secondary roots and buds, which lengthen to form flowering shoots. The structure of this root has been described by Drude (11), Kamienski (39), and Queva (62). The outer epidermal cells become completely filled with hyphae and fall off. The cortex consists of 8–10 layers of cells that are much larger than the epidermal ones. The endodermis is composed of small cells with thickenings on the radial walls in the younger roots, but is indistinguishable in the older ones. The fibrovascular cylinder is composed mainly of thin-walled cells, there being only 3–4 patches of xylem (Kamienski). Material that the writer examined showed

four small areas of xylem. These patches consist only of 1–3 cells, generally reticulate tracheids, no vessels being present according to Kamienski. Drude reports the presence of spiral vessels. The writer has not seen any of the latter. Within the small circle formed by these four xylem elements occurs a parenchymatous mass of pith. Between and outside of the xylem patches is a comparatively large amount of phloem, composed of thin-walled cells, a few sieve tubes with slightly thick walls being present. These sieve tubes are described by Kamienski as having no true sieve plates, but that these are replaced by transverse partitions, and that the walls are thin at certain points. They are easily distinguished by their more granular contents. Secondary thickening occurs; Kamienski states that no cambium is present, and that the secondary tracheids are disposed either singly or in groups toward the pith or sometimes away from the pith. The phloem also gradually increases in the number of cells, until they join to form a ring around the wood. Queva (62), on the other hand, describes the secondary wood as being formed only in a centrifugal direction—outside of the primary tracheids—and that after this, cambial arcs form and produce a continuous ring of xylem and phloem. Older roots examined by the writer showed an increase in the number of xylem elements and between the xylem and the phloem a layer of thin-walled cells resembling a cambium. The roots were not old enough to show the continuous ring of xylem and phloem described by Queva.

No complete description of the old root of *M. uniflora* has been found by the writer. The epidermal cells become filled with hyphae, but do not appear to drop off as soon as in *M. hypopitys*. The mycelial sheath still surrounds the oldest part of the root. The fibrovascular cylinder has a very irregular distribution of elements. The 3–4 single tracheids in young roots have increased in number, until there is quite a large area of wood, mostly reticulated tracheids. The secondary growth in thickness, from the material examined, seems to occur in the manner described by Queva for *M. hypopitys*.

In the least saprophytic ones the epidermis soon dies and falls off, carrying with it the fungal hyphae as in *Chimaphila* and *Pyrola*. In *Monotropa* and especially *M. uniflora* the epidermis is still living and filled with hyphae when the root

is quite old. The less saprophytic ones have a fair amount of wood developed and a comparatively small amount of phloem as seen in *Chimaphila* and *Pyrola*. In *Sarcodes*, *Pterospora*, and *Monotropa* the wood is less developed, the amount of phloem being considerably greater. This greater production of phloem and reduction in the amount of wood is characteristic of saprophytic plants.

The Rhizome

Transverse and longitudinal sections of the underground rhizome of *Chimaphila umbellata* were examined. On the exterior is an epidermis composed of somewhat rectangular cells (on transverse section) with rounded angles and thick walls. The outer wall is much thicker than the others and has on its exterior a layer of ridged cuticle. Interior to this is the cortex, composed of 7–9 layers of rounded thin-walled cells. The walls of the outer two layers of the cortex and those of the epidermis become thickened, forming a cork-like region, so that in cutting sections these all split off together. The cortical cells gradually increase in size toward the interior. The innermost layer, the endodermis, is composed of narrow rectangular, but somewhat irregular, cells. These are thin-walled and show in section four to five cells filled with tannin. Internal to this is the fibrovascular system with an external small area of phloem and much larger area of wood. The pitted vessels appear square on transverse section and there are numerous uniseriate medullary rays through the wood. In *C. umbellata* there were found as many as four annual rings, an evidence that the rhizome is perennial. Inside the wood is a cylinder of rounded thin-walled cells, the pith; starch grains occurring as either single or aggregate clusters are numerous in the epidermis, cortex, and pith.

The structure of the rhizomes of *C. maculata*, *P. rotundifolia*, *P. elliptica* is very similar to that of *C. umbellata*. Conglomerate crystals are present in *P. rotundifolia* and *P. elliptica* but absent in *C. umbellata* and *C. maculata*. There is no rhizome in *Moneses uniflora* or *Monotropa*.

The Ascending Axis

Transverse sections of all the species of Pyrolaceae and Monotropaceae investigated were taken at the base of the ascending axis just below the lowest set of scale leaves.

In *Chimaphila umbellata*, the outline of the section is rounded pentagonal. The epidermis is papillate, the cells having a thick cuticle covered with wax. The epidermal cells and four layers of the cortex beneath have rather heavy thickened walls, so that this appears as a corky tissue. Inside this region are about four more layers of rounded, thin-walled cortical cells, and then the endodermis, a layer of narrow rectangular cells with the radial walls thickened. Within this is a narrow zone of phloem and a much wider one of wood. The material examined shows three annual rings. There are five groups of primary bundles toward the interior. Innermost is the pith composed of thin-walled rounded cells. These cells and those of the cortex contain numerous conglomerate crystals and aggregate starch grains.

In *C. maculata*, the sections resemble closely those of *C. umbellata*, except that the outline is rounded triangular; there are not as many thick-walled layers of cortex; there are only three groups of primary bundles present; and crystals are not as numerous as in *C. umbellata*.

In *P. rotundifolia*, the outline is rounded triangular; the epidermis is not papillate, the cells being only slightly curved outward; only the two outer layers of the cortex are thickened; there are 7–9 layers of unmodified cortex; crystals appear to be present in the cortex only. There are no distinguishable groups of primary bundles; otherwise the section appears like that of *C. umbellata*.

In *P. elliptica*, the structure is almost exactly similar to that of *P. rotundifolia*.

The axis of *Moneses uniflora* is not as thick and woody as those preceding. The outline is circular. The epidermal cells are only slightly curved outward. They and the outermost layer of the cortex are only slightly thickened but not nearly as much as in *Pyrola* and *Chimaphila*. There are about six layers of cortex in all. The endodermis resembles those of the preceding. There is a small amount of phloem, one year's growth of wood with four groups of primary bundles toward the interior, and a small area of pith. Single and aggregate starch grains are found in the cortex and pith, but there appear to be no crystals present.

The structure in *Monotropa hypopitys* is greatly simplified. The section is circular and wider in diameter than in any of the

preceding, as in *Monotropa* the axis becomes fleshy. The epidermal cells are not papillate, and have a cuticular and waxy covering which is not as thick as in *Chimaphila*. There is no outer thick-walled area of cortex. It is composed of about ten rows of large thin-walled hexagonal cells, some of which have slightly thickened walls and contain tannin. The innermost layer of the cortex consists of narrow elongated cells—the endodermis. The central vascular cylinder consists of several bundles separated from each other by medullary rays. Each consists externally of a wide patch of phloem—equal in width to that of the wood. The wood consists of 10–15 cells in each group. Those according to Kamienski (39) are tracheids with either spiral or annular thickening. This ring of wood consists of both primary and secondary wood.

The structure in *M. uniflora* is exactly similar to that of *M. hypopitys*.

Sections of the base of the ascending axis of *Pleuricospora fimbriolata* were taken from boiled up herbarium material. The cortex is wider than in *Monotropa*. The vascular cylinder is more united than in the others, there being a continuous ring of phloem and an almost solid interior of wood—the pith being very small in amount. The wood is much greater in amount than in *Monotropa*.

Epidermis

The epidermis was examined at the middle of the ascending axis or flowerstalk. In *C. umbellata*, it is composed of rectangular cells with thick walls and with an exterior covering of ridged cuticle. Chloroplasts occur in the cells. Small papillae, also with ridged cuticle, are present on some of the cells. Stomata are present, but not numerous. They are small and appear normal and functional; some are of the normal type with the slit parallel to the longitudinal axis—others show all stages of twisting of the guard cells until the opening between them becomes exactly transverse. The series is the same as in *M. uniflora* except that in the latter the guard cells are greatly enlarged and distorted. These transverse stomata are present on the stems of *Viscum album*, *Arceuthobium*, *Antidaphne*, *Loranthus*, *Lepidoceras*, *Nuytsia* of the Loranthaceae; *Choretrum*, *Mida*, *Myoschilus*, *Anthobolus*, *Santalum album*,

Thesium of the Santalaceae; *Cassytha* of the Lauraceae; *Salicornia*, *Casuarina*, *Staphylea pinnata*. The first three groups are all, with the exception of *Nuytsia*, parasitic, so that the presence of transverse stomata on the stem may indicate an abnormal system of nutrition.

In *C. maculata* the epidermis is almost exactly similar to that of *C. umbellata*, except that the papillae seem slightly longer and have somewhat thicker walls.

In *P. rotundifolia* the epidermal cells are longer and thinner walled; there are no papillae; stomata are more numerous and are mostly of the longitudinal slit type.

The epidermis of *P. elliptica* is similar to that of *P. rotundifolia*, except that stomata are very rare and in all pieces of epidermis examined were of the longitudinal type.

In *Moneses uniflora* there are papillae present as in *Chimaphila*. The epidermal cells are long, narrow, and thin-walled, and contain chloroplasts as in the preceding. In all the material examined the writer found no stomata present.

In *Sarcodes sanguinea* the epidermal cells are also long, narrow, and thin-walled. Oliver states that no stomata are present on the flower stalk (the ascending axis), but the writer finds that, though rare and somewhat distorted, stomata are undoubtedly present. Simple stomata with a longitudinal slit as in *M. hypopitys* (Fig. 4, 4) occur. Others have the guard cells twisted around so that the slit is diagonal (Fig. 4, 2). Others are remarkable in that they have three guard cells (Fig. 4, 3). At the base of the axis a few glandular hairs are present. These increase in number toward the top of the flower stalk. They are multicellular with a thick stalk and a slightly rounded head.

In *Pterospora andromedea* the epidermal cells are similar to those of *Sarcodes*. This is the only member of the Monotropaceae up to the present that has been described as possessing stomata on the flower stalks. MacDougal (48), p. 38, states "*Pterospora* is the only dicotyledonous plant without chlorophyll beside *Cotylanthera* that is furnished with stomata." These stomata are of the normal type with the slit parallel to the longitudinal axis. They are very rare. Hairs of two types occur on the flowerstalk; simple uniseriate hairs composed of 3–4 elongated cells the last one club-shaped; glandular hairs with a multicellular stalk and a multicellular club-shaped head.

In *Monotropa hypopitys*, the epidermal cells are similar to those preceding. Stomata are present though rather rare. Previous investigators are unanimous in saying that stomata are absent on the flowerstalk (9. 48, 73). The writer finds two types of stoma—the normal type with the slit parallel to the longitudinal axis (Fig. 4, 4) and that with the slit transverse to the longitudinal axis (Fig. 4, 5). The first type is

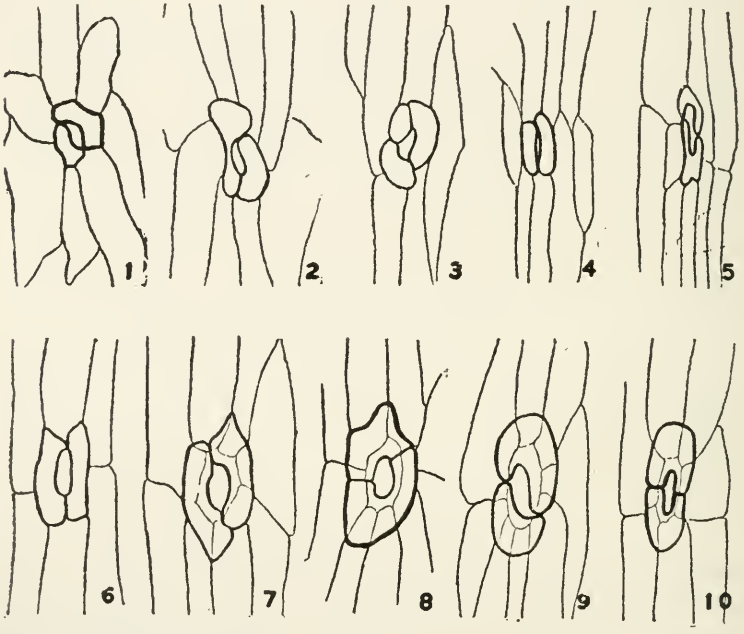

Fig. 4. Stomata × 290.
1. On lower epidermis scale of *Monotropa uniflora*
2–10. On epidermis of ascending axis of:
2–3. *Sarcodes sanguinea*
4–5. *Monotropa hypopitys*
6–10. *M. uniflora*

more frequent in *M. hypopitys*. The guard cells are extremely large and often much distorted. Whether or not these stomata function one cannot say, but their presence indicates that they were functional at one time, at least when the plant was young and before the guard cells were pulled apart by the rapid upward growth of the flowerstalk. Unicellular hairs with ridged cuticular thickenings are present on the epidermis.

In *M. uniflora* the epidermal cells are similar to those of *M. hypopitys*. The transverse type of stoma is much more frequent, the longitudinal type being rather rare. Fig. 4, 6–10 shows a series in the formation of a transverse stoma from the longitudinal. 6 is a normal stoma. In the growth of the stalk the guard cells gradually become pulled apart and slightly turned around as in 7. In 8 the slit is diagonal, 9 shows the cells almost completely around, and finally 10 shows the directly transverse slit.

Portions of the epidermis of boiled-up material of *Pleuricospora* were found to have shorter thicker walled cells than the preceding. No hairs or stomata have as yet been seen but the material at hand was limited, so this does not finally preclude the possibility of their occurrence. Hairs similar to those found on the axis in Pyrolaceae and Monotropaceae are characteristic of many of the Ericaceae. This is another close similarity found in the three families.

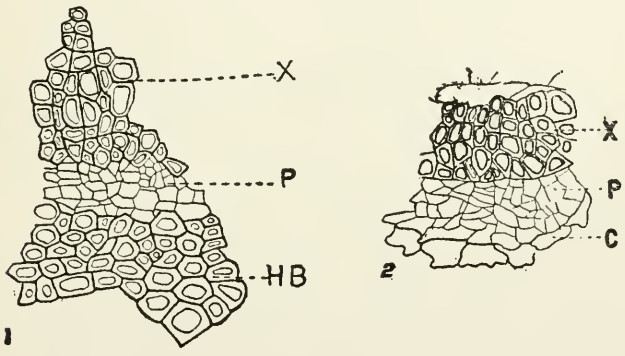

Fig. 5. Transverse section of ascending axis, showing sector of fibrovascular system × 200.
1. *Chimaphila umbellata*
2. *Pleuricospora fimbriolata*
X = xylem; P = phloem; HB = hard bast; C = cortex.

Transverse sections of the ascending axis were taken at a point half way between the flower or flowers and the leaves, or in the Monotropaceae half way between the flowers and the base of the ascending axis.

In *C. umbellata* the epidermis appears as a hollow cylinder of oval cells with a thick outer cuticle and covering of wax. The

papillate hairs appear on transverse section. Internal to the epidermis are two to three layers of thick-walled, then two to three layers of thin-walled, cells forming the cortex. The outer 3–4 layers of the phloem are heavily lignified forming an area equal in width to the succeeding area of thin-walled phloem. There is only one year's wood developed, but this is rather large in amount (Fig. 5, 1), the entire area being one and a half times in width that of soft and hard bast together. Internal to the wood is a rather large area of pith composed of thin-walled rounded cells with small intercellular spaces.

In *C. maculata* the epidermal papillae appear more numerous and more strongly developed than in *C. umbellata*. There is an outer thick-walled area of three layers and an inner thin-walled area of 3–4 layers of cortex. There are four layers of thick-walled hard bast which is slightly greater in width than the soft bast. The wood is not as strongly developed as in *C. umbellata*, the width being equal to that of the soft and hard bast combined. The pith is similar to that of *C. umbellata*.

In *P. rotundifolia* the epidermis is not papillate. There are two layers of thick-walled, three of thin-walled, cortical cells. The hard bast is five layers in thickness, being much greater in width than that of the soft bast. The wood is developed about as much as in *C. maculata*, being equal in amount to the width of the hard and soft bast together.

In *P. elliptica* the appearance of the section is very similar to that of *P. rotundifolia*.

In *Moneses uniflora* the epidermis is not papillate. All the cortical layers (5–6) are thin-walled. There are four to five layers of hard bast that dip in slightly between the patches of soft bast so that the latter does not form a continuous ring as in all the preceding. Each patch consists only of a few small thin-walled cells. Internal to these is a ring of wood that is very poorly developed in comparison with all those preceding. In width it is only slightly greater than that of the soft bast patches.

In *Monotropa hypopitys* the axis becomes more fleshy and wider in diameter than in any of the preceding. There are papillate hairs present that are more numerous and much longer than in *Chimaphila*. Internal to the epidermis are about twenty

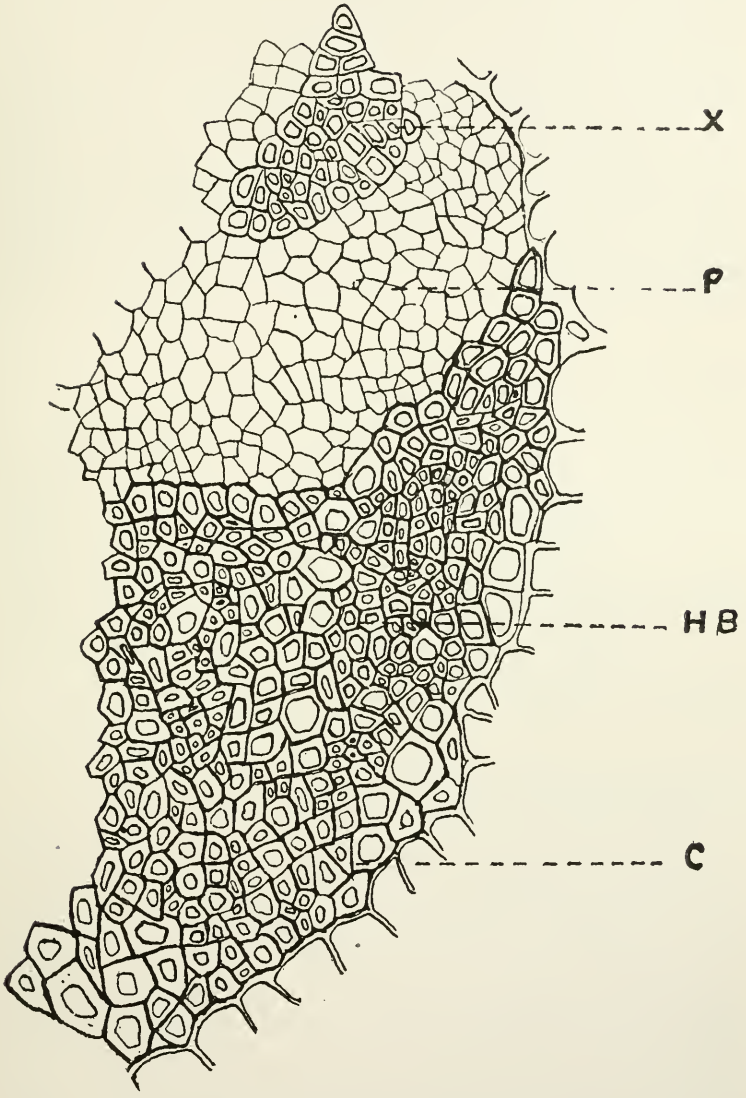

Fig. 6. T. S. ascending axis *Pterospora andromedea* × 200.

layers of rounded thin-walled cortical cells. There is a very great development of hard bast (about 8–9 layers) which dips in between the numerous phloem patches and joins with the indurated medullary rays. It is greater in width than the soft bast, which is well developed in this species. The latter has a width about twice that of the wood, which is extremely reduced in amount, there being only about five to eight cells in a group interior to the many celled phloem patch.

The structure in *M. uniflora* (Fig. 7) resembles that of *M. hypopitys* except that no hairs are present on the epidermis, and the amount of hard bast is not as great, there being only about 4–5 layers.

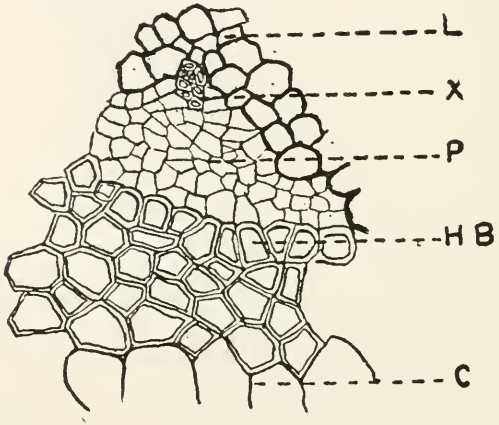

Fig. 7. T. S. ascending axis *Monotropa uniflora* × 200.
L = lignified pith.

MacDougal (48) describes the structure of the ascending axis of *Pterospora andromedea* as follows: "The epidermis is composed of elongated spindle-form elements. The epidermis and the two underlying layers are slightly lignified. The outline is exceedingly crooked, and shows deep invaginations directly over large air-chambers, while in other places distinct fixed stomata are to be found. The cortex is composed of cylindrical elements arranged in circles with intercellular spaces which increase in size outwardly. The fibrovascular bundles contain one or two annular and two or three spiral vessels, with a few alongated elements of slight differentiation, which are perhaps

tracheides. A number of closed sieve tubes are present. The xylem bundles do not form a ring, but immediately external to the bast-region is a complete cylinder of heavy sclerenchyma composed of ten to fifteen layers of cells. Both the xylem and the sclerenchyma are distinctly lignified. The medulla is from 3 to 6 mm. in diameter, making up about half of the cross section of the stem, and is composed of cylindrical elements with ample intercellular spaces." In the material examined by the writer (Fig. 6) the hard bast area was found to be composed of even more than fifteen layers of cells. The phloem was found to be greater in width than the xylem. The xylem in *Pterospora* is better developed, *i. e.*, has more cells and more heavily thickened walls, than in *Monotropa*, but is less so than in *Pleuricospora*.

Sections of the axis of *Pleuricospora fimbriolata* were taken from a boiled-up herbarium specimen. The axis is wider than in *Monotropa*, about the same thickness as in *Pterospora*, and consists mainly of cortex and pith composed of rounded thin-walled cells. The vascular system (Fig. 5, 2) forms an irregular ring placed nearer the exterior than the center of the section. No hard bast is present; the area of soft bast is about equal to that of the wood which is better developed than in any other members of the Monotropaceae examined, there being more cells and the walls more heavily thickened.

According to Solereder (73), the axis of *Schweinitzia odorata* resembles that of *Sarcodes* and *Pleuricospora* in that it does not possess a ring of hard bast fibers.

Sections of the axis of *Sarcodes sanguinea* were cut some distance below the middle. They showed a great increase in size over any of the others examined. The main bulk of the axis is made up of thin-walled cells of the cortex and pith. The bundles as in *Pleuricospora* form an irregular ring which in position is nearer the exterior than the center. There is no hard bast produced in *Sarcodes*. In the section examined by the writer, the phloem was about equal in width to the xylem. The phloem forms a continuous ring; the groups of xylem being separated from each other by medullary rays. Oliver (58), Fig. 49, figures three of these bundles. At the level where he examined it, the phloem is less in extent than the xylem. He states that the bundles undergo no secondary thickening.

In comparing *Monotropa*, *Pterospora*, *Pleuricospora*, and *Sarcodes*, these have been considered in order according to their relative fleshiness and size. The series, given in order of their relative structure from the least simplified to the most simplified, taking as a basis of comparison the relative amount of phloem and wood produced, would be *Pleuricospora*, with a continuous ring of well developed wood equal in width to the phloem, *Sarcodes* and *Pterospora*, with the wood not continuous and not so strongly developed but equal in width to the phloem, then *Monotropa*, with the wood only present in small patches of about five to eight cells in a group and the phloem very well developed.

Sections of the axes of the youngest shoots of some typical ericaceous plants were examined. These resemble closely those of *Chimaphila* and *Pyrola*. In *Ledum groenlandicum*, *Gaultheria procumbens*, *Rhododendron lapponicum*, the epidermis and one to two outer layers of the cortex are thickened just as in *Chimaphila* and *Pyrola*. The inner cortex is less regular, there being wider and more irregular intercellular spaces than in *Chimaphila* and *Pyrola*. There is a ring of hard bast present as in nearly all the Pyrolaceae and Monotropaceae. The wood is generally wider than in *Chimaphila*. The pith is slightly different, there being present trabeculae of thicker walled cells. No comparison can be made between *Chimaphila* and *Pyrola* on the one hand, and older sections of ericaceous plants, as none of the former lives over four years and many of the latter live for many years becoming very woody.

As regards the structure of the epidermis, cortex and the development of cork tissue there is a complete series from shrubby Ericaceae to the most simplified soft fleshy types of Monotropaceae. In *Rhododendron lapponicum* no cork cambium is developed until the third or fourth year when one develops out of phloem tissue. This origin of the cork cambium has been reported by Vesque (82). Layers of cork are laid down and all of the external cortex and epidermis fall off. In the more woody Pyrolaceae, *Chimaphila* and *Pyrola*, there is a tendency for the outer thicker-walled layers of the cortex to separate from the rest during the second and following years. As the plant only lives for 3–4 years no opportunity for the formation of a cork cambium takes place. In the saprophytes

which live above ground only one season, there is no separation of the cortex even suggested. *Pterospora* is reported by MacDougal to have the epidermis and the two outer layers of the cortex slightly lignified, but in the others the cells are not at all thickened.

The structure of the axis also illustrates a gradual descending series from typical Ericaceae, with strong development of wood, to *Chimaphila*, which is almost as woody as some of the sub-shrubby Ericaceae, to *Pyrola*, which is less woody, to *Moneses*, with still less wood developed, then with a still decreasing amount of wood development through *Pleuricospora*, *Sarcodes*, *Pterospora*, and finally to *Monotropa*, where the wood is extremely small in quantity and the phloem well developed.

The Leaf

In *C. umbellata* the stem produces above ground alternating groups of 2–3 scale leaves and whorls of 3–5 foliage leaves. The leaves persist for four years. The last whorl of leaves and the inflorescence appear in the same year so that no scale leaves occur between the youngest whorl of leaves and the inflorescence. The leaves are leathery, somewhat narrow at the base, becoming wider above with a serrate margin, dark green above, lighter below.

In *C. maculata*, there is the same alternating arrangement of scales and leaves as in *C. umbellata*, except that only three or four foliage leaves are produced in a whorl. The inflorescence does not appear in the same year as the last whorl of leaves as in *C. umbellata*, so that above these at the base of the flowerstalk three scales are borne. These are the scales which protected the inflorescence over the preceding winter. The leaves are leathery, lanceolate, with an acute apex, serrate, dark green above (though lighter than in *C. umbellata*), with white spots especially along its midrib, and rather reddish green beneath.

In *P. rotundifolia*, the arrangement of scales and leaves is like that in *Chimaphila*, except that one to three foliage leaves may be produced in one year, and that these are not arranged in a whorl as in *Chimaphila*. The leaves are evergreen, lasting from two to four years, and the node between two successive years leaves is short, so that the leaves of two to three years appear to be in a common rosette. They have long, narrowly

winged petioles, and large orbicular crenulate, prominently veined, dark green, leathery blades.

In *P. elliptica*, there occurs the same succession of scale leaves and foliage leaves, ending with three scale leaves at the base of the flowerstalk, this arrangement being characteristic of the genus. The leaves are evergreen, lasting from two to three years. They have narrowly winged petioles, shorter than in *P. rotundifolia*, and large elliptic crenulate blades, which are smaller in size, less prominently veined, lighter green, and less leathery than in *P. rotundifolia*.

In *P. secunda*, the leaves are evergreen and smaller than in *P. elliptica*. The petioles are shorter, the blades much less leathery, and lighter green in color.

In *P. minor*, the leaves are evergreen and of the same size, or smaller than in *P. secunda*.

In *P. chlorantha*, the leaves are evergreen and of the same size or smaller than in *P. minor*.

In *P. aphylla* Holm (30) has described and figured a rosette of small green leaves "provided with a distinct petiole and a blade varying from lanceolate to broadly ovate, obtuse or slightly pointed." Below these occur a few scale leaves, and above them the bud for the next year's inflorescence. The green leaves are deciduous and are produced in alternate years with the flowering shoot. For this reason some have incorrectly described the plant as aphyllous. Lateral inflorescences, which arise in the axil of a scale, occur, and are therefore not preceded by green leaves.

In *Moneses uniflora*, the arrangement of alternating whorls of scales and leaves is similar to that of the genus *Pyrola*. The leaves, though not at all leathery, are evergreen for two to three years. They are small elliptic, acute, with a serrate margin.

In *Pterospora andromedea*, the leaves are reduced to brownish scales arranged closely together, in fact overlapping at the base of the flowering axis, but becoming more distant from each other toward the region where flowers are produced. Those at the base of the stem are small and somewhat triangular. Further up the axis, these become narrower and longer, and finally they decrease in size toward the flowers. Those at the base are smooth on the outer (lower) surface, but toward the top of the flower axis they become more and more hairy gland-

ular. Stalked glandular hairs occur on the margins of all scales.

In *Sarcodes sanguinea*, the leaves, as described by Oliver (58), "show a gradual transition in form from the small scales at the base to the thick fleshy ones covering the greater part of the vegetative portion of the shoot. These again pass over into the linear bracts. The leaves and bracts are fringed with stalked glands." The outer surfaces of the leaves toward the base of the flower stalks are smooth; toward the tip they become slightly pubescent, the flower bracts becoming quite markedly pubescent. All the leaves and bracts are crimson in color.

In *Monotropa hypopitys*, the leaves are reduced to small oval-triangular, somewhat thick, yellow, slightly puberulent scales, pressed tightly against the flowering axis. They are arranged closely together at the base of the flower axis, but become separated further up.

In *M. uniflora*, the leaves are like those of *M. hypopitys*, except that they are white and glabrous and much more membranous.

In *Pleuricospora fimbriolata*, the leaves are likewise reduced to pale brownish scales that are small, imbricating at the base, but become larger and more distant from each other above. They all have hair-like processes on their margins, resembling somewhat an incompletely developed stalked gland of *Sarcodes*.

This reduction of leaves to scales and the general arrangement of these are similar in *Allotropa*, *Schweinitzia*, and *Newberrya*.

In typical Ericaceae, as in the Pyrolaceae, there is produced, after the foliage leaves of one year, a leaf or flower bud covered with bud scales. This gives the alternating series of scale leaves and foliage leaves seen in the Pyrolaceae. In the Ericaceae the scales are deciduous, falling off shortly after the leaves unfold. In the Pyrolaceae, they are persistent and green, or greenish membranous for the season, then becoming brownish and lasting for 2–4 years. This persistence of the scales through the season also occurs in all members of the Monotropaceae. Here they are enlarged and take the place of foliage leaves.

In Ericaceae the foliage leaves are always green and usually quite leathery, in most also evergreen for two or more years. The genus *Chimaphila* and some of the Pyrolas, *i. e.*, *P. rotundifolia*, are also evergreen and leathery, but in other species of

Pyrola the leaves become less leathery until in *P.* (*Moneses*) *uniflora* the leaf has a characteristic deciduous structure but is still evergreen. In *P. aphylla*, the foliage leaves are deciduous, and the ascending axis, which bears the flower, produces only scale leaves along its course. This species is a connecting link between the evergreen type and that of all the members of the Monotropaceae, where no foliage leaves are produced, their place being taken by expanded fleshy scale leaves.

The question arises as to whether the scale leaves in the Monotropaceae are the homologues of the scale leaves, or of the foliage leaves in Ericaceae and Pyrolaceae. In the writer's opinion, they represent both scale leaves and foliage leaves. The deciduous scale leaves of the Ericaceae have gradually become green and persistent, then expanded, enlarged and much more numerous. The green leaves have become smaller and all have changed in color from green in the Ericaceae and Pyrolaceae to brownish in *Pterospora*, crimson in *Sarcodes*, pinkish yellow to yellow in *M. hypopitys*, to pinkish white or white in *Monotropa*.

The Leaf—Microscopic Structure

The microscopic structure of the leaf of *C. umbellata* has been described and figured by H. E. Petersen (60). His material was collected in Denmark, but corresponds according to his description and figures almost exactly with the material examined by the writer. The epidermis, both upper and lower, is heavily cuticularized, and, on the surface of this, a layer of wax is present. (The latter is not mentioned by Petersen.) The epidermal cells are rectangular on transverse section, wavy walled on surface view. There is a three-layered palisade tissue beneath this, and a spongy mesophyll composed of thin-walled, branched cells with large intercellular spaces. Stomata are present on the lower epidermis on the same level as the other epidermal cells. Petersen reports the presence of starch in both the upper and lower epidermis, and the absence of hairs and hydathodes. Starch is very plentiful in both palisade and spongy mesophyll, though he does not make note of this. He also does not mention the presence of conglomerate crystals of calcium oxalate, which the writer finds occur in large numbers throughout the spongy mesophyll. These occur as small con-

glomerate crystals, about one-third the size of a normal mesophyll cell, and as much larger masses, completely filling an enlarged mesophyll cell. They are mentioned by Rommel (65) who has also given a short description of the microscopic structure of the leaf similar to Petersen. Both of these descriptions, however, deal with only the laminar portion of the leaf.

At the midrib, the halves of the lamina form an angle of 90°, and the leaf extends out into a ridge. The upper epidermis is similar to that over the lamina, consisting of rectangular cells (on transverse section) with thickly cuticularized walls, especially on the outer surface. Beneath the upper epidermis, the palisade tissue thins out to only one layer of cells, that are almost isodiametric. Immediately below this is the midrib vascular bundle. Within the bundle sheath is a fan-shaped area of xylem, below which is a narrower region of phloem, composed of a narrow area of soft, and a wider area of hard, bast. Beneath the bundle are two layers of spongy parenchyma cells, which are round, somewhat thick-walled, and closely packed together. Next to this is one layer of rounded cells, pressed tightly against the lower epidermis. The walls are rather heavily thickened, so that in cutting they easily break away from the rest of the spongy mesophyll. The lower epidermal cells, at the midrib region, become less rectangular, more isodiametric than in the laminar portion, the cuticle of each cell swelling out somewhat, so that the outline of the lower epidermis in transverse section becomes crenulate.

C. maculata, while showing essentially the same type of leaf as *C. umbellata*, differs slightly in structure. The upper epidermis consists of wavy walled cells, in surface section, appearing rectangular in transverse section, except that the outer face of each cell protrudes from the surface forming a short rounded papilla. This is, however, confined to the upper epidermis, the cuticle of the lower being perfectly flat as in *C. umbellata*. Chloroplasts occur in both upper and lower epidermis, no hairs are present, and stomata, similar in form to those of *C. umbellata*, but projecting slightly from the epidermis, occur on the lower surface. The palisade tissue consists of but two layers of elongated cells. The spongy mesophyll has several layers of irregularly branching cells with large intercellular spaces. Both palisade and spongy mesophyll cells are

filled with starch grains; small and large conglomerate crystals of calcium oxalate, exactly similar to those of *C. umbellata*, occur in the spongy mesophyll.

At the midrib the laminar halves form an angle of 135°–180°, the leaves being almost entirely flat, but with a ridge on the lower epidermis, similar to that of *C. umbellata*. The upper epidermis is of the same appearance as that over the lamina. The palisade still consists of two layers, but the cells are shorter and wider. Beneath this are one to two layers of spongy mesophyll. The midrib bundle is very similar in appearance to that of *C. umbellata*. Under the bundle are three layers of spongy mesophyll cells, closely packed together and with slightly thickened walls similar to those of *C. umbellata*, as is also the layer just next to the lower epidermis, with its rounded thick-walled cells, closely packed together and pressed against the lower epidermis. The cells of the latter have become shorter, more isodiametric, and have their outer walls curved outward slightly.

The microscopic structure of the leaf of *P. rotundifolia* has been described by Rommel (65), and of *P. rotundifolia* var. *grandiflora* by Petersen (60). The material examined corresponds fairly well with both of these descriptions except that the writer finds stomata, not hydathodes, on the upper epidermis; chlorophyll grains in the upper epidermal cells; crystals, both small and large, in the mesophyll (Petersen does not mention them, and Rommel states that they are absent); and no differentiation into palisade and spongy mesophyll. The epidermis is covered by a thin cuticle (much less than in *Chimaphila*) and a layer of wax. Both upper and lower epidermis consist of wavy-walled cells on surface section, rectangular in transverse section, and contain chloroplasts. Numerous stomata are present on the lower epidermis, projecting slightly from the level of the other epidermal cells. They are fairly frequent on the upper epidermis, especially toward the margin of the leaf. The mesophyll consists of five to six layers of closely packed thin-walled cells. Rommel describes the mesophyll as having smaller intercellular spaces near the upper epidermis, and larger intercellular spaces near the lower epidermis. Petersen's figure (p. 81) also illustrates this, but the writer's material shows no difference between the upper and

lower mesophyll. There is, however, the distinct transparent median non-tannin-containing layer of the mesophyll described by Petersen for his Danish specimens of *P. rotundifolia*. The mesophyll cells, beside containing starch and tannin, contain crystals similar to those of *Chimaphila*. At the midrib, the leaf becomes prominently ridged on both surfaces. The upper epidermal cells become enlarged and have a much thicker layer of cuticle and wax than over the rest of the lamina. The first layer of mesophyll cells become packed closely together and against the upper epidermis. There are four to five layers of rounded thin-walled cells, above and below the midrib bundle. The latter closely resembles that of *Chimaphila*. The lowermost layer of mesophyll also consists of rounded, thick-walled, closely packed cells, tightly pressed against the lower epidermis. The latter has its cells enlarged and has a thicker cuticle than on the laminar region.

In *P. elliptica*, the structure of the lamina is exactly similar to that of *P. rotundifolia*, except that the cuticle with its covering of wax is much thinner and that on the upper epidermis is slightly thicker than that on the lower epidermis. At the midrib, the structure is again like that of *P. rotundifolia*, except that the cuticle is thinner.

The structure of the leaf of *P. secunda* has been described by Petersen and Rommel and figured by the former, p. 85. The type of leaf is very similar to that of *P. rotundifolia*—there is no differentiation into a palisade and a spongy mesophyll. The cuticle, according to Petersen, is thicker than in *P. rotundifolia* (this is not true of the writer's material) and stomata are present also on the upper epidermis. Rommel fails to note the latter, and also states that no crystals are present. At the midrib, the leaf is ridged above, but not as much as in *P. rotundifolia*.

The structure of the leaves of *P. media* and *P. picta* has been described by Rommel. These are similar to *P. rotundifolia* for there is no palisade mesophyll. He states that crystals are absent in these.

The leaf of *P. minor* has been described and figured (p. 83) by Petersen as having an undifferentiated mesophyll like *P. rotundifolia*, but Rommel states that there is one layer of palisade tissue. The writer finds the structure of the leaf to be similar

to that of *P. rotundifolia*—no palisade tissue being present. In some places, however, a few of the cells of the layer next to the upper epidermis become slightly elongated, as if a palisade was beginning to form, or rather as if these were the few remaining cells of what was once a palisade layer. Rommel notes the presence of crystals. Petersen mentions the presence of stomata on the upper epidermis, a fact not stated by Rommel. The writer finds stomata on both upper and lower epidermis, protruding slightly from the level of the epidermis. At the midrib the leaf is ridged above and below, but even less than in *P. secunda*. The bundle is not as strongly developed as in *P. rotundifolia*.

In *P. chlorantha*, Rommel states that there is one layer of palisade mesophyll, and that crystals are present. The writer's material agrees with this. The epidermal cells are wavy-walled on surface view, rectangular in transverse section. Stomata are present on the lower surface only. There are one layer of palisade and four layers of spongy mesophyll with larger intercellular spaces than in *P. rotundifolia*. At the midrib there is only a slight curving upward and a small downward ridge. The bundle is similar to that of *P. minor*.

In *P. aphylla*, Holm (30) describes the leaf as having a normal epidermis, covered by a thick and wrinkled cuticle, stomata are present on both upper and lower epidermis, but more numerous on the lower epidermis. He reports the presence of two layers of palisade tissue and a spongy mesophyll of loosely connected cells with large intercellular spaces.

In the genus *Pyrola*, most of the species examined, *i.e.*, *P. elliptica*, *P. secunda*, *P. media*, *P. picta*, conform to the type of *P. rotundifolia* with non-differentiated mesophyll. *P. minor* seems to show a transition toward the formation of a palisade. *P. chlorantha* shows one layer of palisade tissue, and *P. aphylla* shows two layers of palisade and a typical spongy mesophyll.

The leaves of *Moneses uniflora* have also been described microscopically by Petersen and Rommel and figured by the former (p. 86). The epidermal cells—wavy-walled in surface section, rectangular in transverse section—have only slightly cuticularized outer walls and contain chlorophyll. Stomata are numerous on the lower epidermis, and are slightly projecting. The upper layer of the mesophyll consists of slightly

elongated cells forming a palisade of one layer. The spongy mesophyll cells branch irregularly and have large intercellular spaces. Starch occurs in all the mesophyll cells. Rommel does not mention the presence of the one layer of palisade tissue. He also states that crystals are not present, while the writer finds that they are present. At the midrib the upper surface of the leaf is curved slightly upward, the lower flat. Both upper and lower epidermis are similar in appearance to that over the lamina. The palisade cells become somewhat shorter. One layer of rounded mesophyll cells occurs between the palisade and the bundle. The midrib bundle is much smaller in extent than in either *Chimaphila* or *Pyrola*, the latter bundles being almost equal in size to the midrib. It consists of a small area of xylem—not radiating as in the others—beneath which are several layers of phloem. Beneath the bundle are two layers of spongy mesophyll cells between it and the epidermis.

MacDougal (48) has described in part the structure of the leaf of *Pterospora andromedea*. He describes marginal stalked glands similar to those on the flowering axis. According to him "The basal scales are flecked with irregular patches of yellowish brown areas, due to the penetration of the epidermal cells by brownish hyphae, which completely fill them and extend over the surface of the scales in a network." In a few scales the writer has seen ramifying hyphae over the surface, but not penetrating the epidermal cells. The epidermis consists of elongated narrow cells that appear narrowly oval on transverse section. Stomata, though not numerous, are present on the lower epidermis. Hairs are present on the lower surface toward the sides of the scale. These are simple unicellular protuberances. The lowermost scales are smooth. Further up the stalk, the scales become more and more hairy until those subtending the flowers have long stalked glandular hairs similar to the marginal ones. These consist of a rather long multicellular stalk with an oval head composed of glandular cells. The mesophyll is composed of numerous layers of thin-walled hexagonal cells. The transverse section is wider at the midrib, the midrib bundle being larger than the others. There is a slight curving upward at the midrib region as in *Moneses uniflora*. The bundles are more reduced than in *Moneses uniflora*. There are several xylem elements present, but the main part of the bundle consists of phloem.

The structure of the leaf of *Sarcodes sanguinea*, described by Oliver (58), corresponds closely with the material examined by the writer. Stalked glands, similar in appearance to those on the flowering axis, appear on the margin of the leaves. The epidermis consists of thin-walled hexagonal cells slightly longer than broad. On transverse section, these appear as somewhat oval cells, those of the lower epidermis being slightly smaller than those of the upper. Both surfaces are covered with cuticle and a thin layer of wax, that on the outer or lower surface being slightly thicker than that on the upper. Stomata are absent. The basal leaves have a smooth lower epidermis, no hairs being present. Further up the flowering axis, the lower surface shows beginnings of multicellular glands with a long multicellular stalk and a club-shaped head. These become more numerous on the bracts which subtend the flowers. The mesophyll is undifferentiated, except that the first layer of cells beneath the epidermis is composed of cells similar to it. Below this occur 17–18 layers of hexagonal, thin-walled, closely packed cells. The transverse section of the leaf is the same throughout, the bundles being all nearly equal in size. They are much more reduced than in *Moneses uniflora*. Several xylem vessels are present, but the main part of the bundle is made up of phloem.

The structure of the leaves of *Monotropa hypopitys* has been described by Kamienski (39). The writer's material corresponds closely with his description, except for the presence of hairs, a fact which he does not mention. His material, however, may have been *M. hypopitys* var. *glabra*. The epidermis consists of narrow elongated cells on surface view, somewhat oval on transverse section, with the outer wall cuticularized, ridged, and with a thin layer of wax on the outside of the cuticle. Hairs are present, few on the upper, numerous on the lower epidermis. They are simple, unicellular outgrowths with small, wart-like protuberances. Stomata are absent on the upper and very rare on the lower epidermis. Solereder (73) mentions that they are rare on the lower surface of the leaf, but all other writers say they are absent. The writer found three to five on a scale. The mesophyll consists of several layers of thin-walled, hexagonal cells with no intercellular spaces. There is no differentiation into palisade and spongy mesophyll. Several bundles almost

equal in size pass through the mesophyll so that at the midrib the scale is only slightly thicker than in the laminar region. The bundle is even more reduced in size and number of elements than in *Pterospora* and *Sarcodes*, the woody tissue consisting only of one to two elements, the main part of the bundle being composed of phloem.

The leaf of *M. uniflora* is exactly similar in structure to that of *M. hypopitys* except that no hairs are present in *M. uniflora* and stomata are even more rare than in *M. hypopitys* (Fig. 4, 1). The writer found only one stoma on the lower epidermis of each leaf.

The leaf of *Pleuricospora fimbriolata* is very similar in its structure to that of *Monotropa*. The epidermal cells are slightly longer than wide on surface view, and oval in transverse section. They are covered by a thin ridged cuticle and layer of wax. No hairs or stomata are present. There are eight rows, at the widest part, of thin-walled, closely packed hexagonal cells. The midrib bundle is only slightly larger than the others and is even more reduced than in *Monotropa*.

From reviewing literature on the structure of the leaves of the Ericaceae (88, 56, 60, 73) and from an examination of sections of the leaves of various members of the family, the writer finds that in general the structure is very similar to that of *Chimaphila*, which the writer considers to be the least saprophytic genus of the Pyrolaceae. The Ericaceae generally agree with *Chimaphila* in having a thick cuticle, often with a coating of wax, a mesophyll differentiated into palisade and spongy regions, and chlorophyll in the upper and lower epidermis. Solereder reports cuticular ridges as a common occurrence in the Ericaceae. Their presence has been indicated in all the Pyrolaceae and Monotropaceae examined. Papillae on the epidermis, except at the midrib, are rare in the Pyrolaceae and Monotropaceae, only occurring in *C. maculata*. They are present, however, on the lower epidermis of *Rhododendron campylocarpum*, *R. thomsoni*, *Kalmia glauca*, *K. latifolia*. At the midrib in typical Ericaceae, the epidermal cells often bulge out to form papillae. This is true of *Chimaphila* and *Pyrola* also.

Stomata in the Ericaceae and Pyrolaceae may be present on the lower surface only, but are frequently present on both sur-

faces. They do not, except in a few cases, have any specially formed subsidiary cells but according to Breitfeld (88) they often extend beyond the surface so that they overlap the surrounding epidermal cells to some extent. This arrangement is also true of those of the Pyrolaceae and Monotropaceae (Fig. 4).

The types of hairs present in Ericaceae are varied; Breitfeld (88, p. 329, Pl. VI), Neidenzu (56, p. 141, Pls. III, IV, V, VI), and Solereder (73, p. 484, 485) have given detailed descriptions and numerous figures of those found in all groups of the Ericaceae. The forms of hairs present in the Pyrolaceae and Monotropaceae are not numerous; in fact, hairs are absent entirely on the leaves of all the Pyrolaceae. In *Pterospora* there are present on the margin of the leaves, stalked glands composed of a multiserrate stalk and a glandular head formed of several cells. This type, according to Solereder, is present in *Arbutus*, *Arctostaphylos alpina*, *A. tomentosa*, *Enkianthus*, *Gaultheria myrsinites*, and *G. hispida*. In *Sarcodes* stalked glands on the margin and also on the lower surface of the upper leaves are very similar in structure to those of *Pterospora*, except that in *Sarcodes* the glandular head is not as enlarged as in *Pterospora*. In *Monotropa hypopitys* another type of hair occurs. It is unicellular, short, blunt, and the waxy covering is somewhat warted. This simple type is common throughout the Ericaceae.

Chlorophyll grains occur in the epidermis of many plants belonging to the Ericaceae and the Pyrolaceae. Petersen reports their presence in the upper epidermis of the leaf of *Rhododendron lapponicum*, the lower epidermis of *Vaccinium vitis-idaea* f. *pumila*, upper and lower epidermis of *Vaccinium oxycoccus*, and states that Lidforss (45) reports their presence in the upper epidermis of *Ledum palustre*, *Loiseleuria procumbens*, *Phyllodoce coerulea*, *Andromeda polifolia*, *Lyonia calyculata*, and in both upper and lower epidermis of *Arctostaphylos uva-ursi* and *A. alpina*. In the Pyrolaceae, Petersen reports their presence in the lower epidermal cells of the leaf of *P. rotundifolia* var. *grandiflora*, and *P. minor*, in both upper and lower epidermal cells of *P. secunda*, *P. uniflora*, *C. umbellata*, and the writer has noted their presence in both upper and lower epidermal cells of *P. elliptica* and *C. maculata*.

The palisade tissue varies in Ericaceae from five to six layers in *Rhododendron lapponicum*, *Vaccinium vitis-idaea* and *Ledum*

palustre; to three to four in *Loiseleuria procumbens, Epigaea repens,* and *Lyonia calyculata;* to two to three in *Ledum groenlandicum, Kalmia latifolia, Agarista revoluta, Diplycosia pilosa,* and *Andromeda polifolia;* to two in *Cassiope hypnoides, Gaylussacia pinifolia, Dendrium buxifolium,* and *Vaccinium uliginosium:* to one in *Vaccinium myrtillus* and *Chiogenes hispidula.*

The Pyrolaceae show a gradual reduction in the number of palisade layers. *Chimaphila umbellata* has three; *C. maculata* two; *P. chlorantha* and *Moneses uniflora* one; *P. rotundifolia, P. secunda, P. minor* all have no palisade tissue developed, nor is it present in any of the Monotropaceae.

Conglomerate and single crystals are common in many members of the Ericaceae occurring in the palisade or spongy parenchyma, or in both. Niedenzu (56) has given a table of their distribution in the Arbutoideae and Vaccinioideae (pp. 175, 176). In the Pyrolaceae only conglomerate crystals occur and these are found in the spongy mesophyll. The writer has found them in *C. umbellata, C. maculata, P. rotundifolia, P. elliptica, Moneses uniflora.* Rommel (65) reports their presence in *P. minor* and *P. chlorantha.* The writer has not found any crystals in the leaves of any of the Monotropaceae examined.

The Inflorescence

In *C. umbellata,* the flowerstalk is about 1 dm. long with no scales. The flowers are arranged in a 2–8-flowered corymb, each flower on a slightly recurved pedicel 8–12 mm. in length. This comes off in the axil of a linear subulate, smooth, deciduous bract.

In *C. maculata,* the flowerstalk is about 1 dm. long with no scales. There are 1–5 flowers arranged in a corymb; the pedicels are pubescent and about 16–18 mm. long. The bracts are linear, about 15 mm. long, with the margin appearing slightly fimbriolate near the apex on microscopic examination.

In *P. rotundifolia,* the entire flowerstalk is 2–3 dm. in length with two scales. There are 6–20 flowers arranged in a raceme, each flower being borne on a smooth recurved pedicel, 6–10 mm. long, in the axil of a lanceolate bract that is 5–8 mm. long. This also, when examined microscopically, shows a somewhat fimbriolate margin toward the apex.

In *P. elliptica*, the flowerstalk is 1–2 dm. in length with 0–2 scales; the raceme is 6–15-flowered; the bracts are linear-lanceolate, 5–6 mm. long, about equal in length to the smooth pedicels. The margin of the bracts is entire.

In *P. secunda*, the flowerstalk is 1–2 dm. in length, with 1–4 scales. The flowers, 6–17 in number, are arranged in a raceme with the flowers all turned to one side. The bracts are subulate-ovate, slightly shorter than the pubescent pedicels, which are 4–5 mm. in length.

In *P. minor*, the flowerstalk is 0.5–2 dm. in length with one or two scales; there are 5–17 flowers borne in a raceme, each on a pedicel equal in length to the 2–3-mm. subulate bracts.

In *P. chlorantha*, the flowerstalk is 0.5–2 dm. in length, with a single scale. There are 2–8 flowers borne in a raceme. The bracts are lanceolate, 4 mm. long, shorter than the pedicels, which are 5–6 mm. in length.

In *P. aphylla*, the flowerstalk is 1–3 dm. in length, with numerous scales extending from the base upward. There are 8–25 flowers borne in a raceme, each on a recurved pedicel about 5 mm. in length. The bracts are lanceolate, 3–5 mm. in length.

In *Moneses uniflora*, the flowerstalk bears one flower and is 0.5–1.3 dm. in length with one scale, similar in form to the one bract. This is ovate, about 4 mm. in length, and, under the microscope, is seen to have numerous unicellular hairs along the margin. The margin becomes slightly fimbriolate toward the apex.

In all members of the Monotropaceae examined, green leaves are not produced, their place being taken by scales which gradually pass with little change of structure into bracts subtending the flowers.

In *Monotropa hypopitys*, the flowerstalk—in this case the entire ascending axis—is 1–3 dm. tall. The flowers are numerous, 3–15, each borne on a pubescent pedicel that is 3 mm. in length. The bracts are narrow ovate, yellow, 10–12 mm. in length, shorter than the flower. The outer surface and the margin of these bracts are covered with unicellular hairs. Toward the apex, the margin becomes somewhat irregularly toothed.

In *M. uniflora*, there is one flower produced at the end of the 0.5–1.5-dm.-tall flowerstalk. The bracts, white in color,

are narrower than the scales below, and are about 10–12 mm. in length, shorter than the flower, and are quite numerous at the base of the flower. They are much thinner in texture than in *M. hypopitys*. No hairs are present in these. The margin becomes somewhat irregularly toothed toward the apex.

In *Sarcodes sanguinea*, the flowerstalk is 1–5 dm. in length. The flowers are numerous, borne in racemes, each on a pedicel that is pubescent with short glandular hairs. Those of the lower flowers are longer than those of the upper. The bracts, crimson in color, become much narrower than the lower scales and are longer than the flowers, 2.5–6 cm. long. The bracts ensheathe the buds as they come above the surface of the ground. Later they curve backward. The whole outer surface and the margins of the bracts are covered with glandular hairs. Near the apex, the margin appears somewhat toothed.

In *Pterospora andromedea*, the flowerstalk is 3–11 dm. in length. The numerous flowers are borne in racemes. The purplish brown bracts are linear, about 5 mm. in length, as long as, or longer than, the pubescent pedicels. Numerous glandular hairs are present on the margin and lower surface.

In *Pleuricospora fimbriolata*, the flowerstalk is 1–2.5 dm. long. Numerous flowers are borne in a raceme. The brownish bracts are smooth, 1–2 cm. long, have a fimbriolate margin.

In *Schweinitzia odorata*, the flowerstalk is 5–11 cm. long. Flowers are borne in a dense terminal raceme. Bracts are purple or purplish brown and about 8 mm. in length.

In *Allotropa virgata*, the flowerstalk is 1–5 dm. long. Numerous flowers are borne in a raceme. The whitish bracts are linear-lanceolate, 1–2.5 cm. in length, narrower than the lower scales.

In *Newberrya congesta*, the flowerstalk is 1–5 dm. tall or less, terminated by a "corymbiform glomerule"; "scales ovate brownish—the upper ones narrower, all obtuse irregularly erose" (72).

In *Newberrya spicata*, the flowerstalk is mostly less than 1 dm. tall, terminated by a dense spike; scales oblong, brownish, sometimes acutish erose fimbriate (72).

In typical Ericaceae, the inflorescence is generally racemose, or condensed to a corymb or umbel as in *Rhododendron*, or solitary axillary as in *Kalmia hirsuta*, *Phyllodoce*, *Cassiope*, *Chiogenes*. In the Pyrolaceae and Monotropaceae, *Pyrola*,

Monotropa hypopitys, *Sarcodes*, *Pterospora*, *Pleuricospora*, *Schweinitzia*, *Allotropa* have racemose inflorescence; *Chimaphila*, and *Newberrya* corymbose; *Moneses uniflora* and *Monotropa uniflora* solitary terminal flowers, thus forming a series parallel to that of the typical Ericaceae.

The bracts in the Ericaceae are generally small, green, often deciduous as in *Chimaphila* and *Pyrola*. In the Monotropaceae, they have become much larger, and like the fleshy scale-like leaves. There is a transition from forms like *C. umbellata* and *C. maculata*, with no scales on the flowerstalk, to *P. rotundifolia*, *P. elliptica*, *P. minor*, *P. chlorantha*, *Moneses uniflora* with 1–2 scales; *P. secunda* with generally 4; *P. aphylla* with still more numerous scales and no, or rarely, green leaves, and finally to *Monotropa*, *Sarcodes*, *Pterospora*, *Pleuricospora*, *Schweinitzia*, *Allotropa*, and *Newberrya*, where the scales are very numerous, fleshy, entirely replacing green leaves at the base and becoming only slightly modified toward the flowers.

In the Ericaceae the plants live for two or more years before flowering and the flower buds appear in the autumn of the year preceding their expansion. This also occurs in all members of the Pyrolaceae. In the Monotropaceae the underground part lives for a year before sending up a flowering axis and buds do not appear above ground until the spring, when they are ready to expand—this of course due to the fact that the ascending axis in the Monotropaceae is annual.

The Sepals

In *Chimaphila umbellata* there are five green sepals united at the base. The lobes are rounded, about 2 mm. in length, and appear entire. Under the microscope, however, the margin appears slightly fimbriolate.

In *C. maculata*, there are five small oval sepals, united at the base. The segments are slightly longer than in *C. umbellata*, being 3 mm. in length, about one-fourth the length of the petals. Simple unicellular hairs are present along the margin.

In *P. rotundifolia* there are five green sepals united at the base. The five lobes are lanceolate acute with spreading tips and are 3–3.5 mm. long, one-half to one-third the length of the petals.

In *P. elliptica*, the lobes of the sepals are much shorter than in *P. rotundifolia;* they are triangular, ovate-acute, about 2 mm. long, not one-fourth the length of the petals.

In *P. secunda*, the calyx lobes are "oval or elliptic, 1 mm. long, rounded at the apex" (72).

In *P. minor*, the calyx lobes are "triangular-acute or short-acuminate, as broad as long" (72).

In *P. chlorantha*, the calyx lobes are "triangular, acutish or obtusish, about as broad as long" (72).

In *P. aphylla*, the calyx lobes are "ovate-triangular, acute, as long as broad, or slightly longer, about 1.5 mm. in length" (72).

In *Moneses uniflora*, the calyx lobes are ovate, obtuse, 3 mm. long, with numerous unicellular hairs along the margin.

In *Monotropa hypopitys*, the sepals are distinct, not united. They consist of 2–3 narrow bract-like structures about 6–8 mm. long, yellow in color, with a few long unicellular hairs on the upper surface and numerous ones on the margin and lower epidermis.

In *Monotropa uniflora*, there are 2–4 white bract-like sepals, 1–1.5 cm. long, which are not united. These are glabrous, except for a few hairs on the upper surface. The margin begins to show a slight irregular toothing near the axis.

In *Sarcodes sanguinea*, there are five fleshy oblong-lanceolate crimson sepals about 2 cm. in length. Oliver states that these are distinct, but the writer finds that they are very slightly united at the base, and have a fimbriolate margin and the entire outer surface covered with glandular hairs.

In *Pterospora andromedea*, the sepals are brownish, united; the lobes are lanceolate, about 4 mm. in length, and are glandular pubescent.

In *Pleuricospora fimbriolata*, the four whitish sepals are separate lanceolate, 8–9 mm. long, and have a fimbriate margin.

In *Schweinitzia odorata*, the sepals are five, purple or purplish brown, becoming lanceolate, 8–12 mm. long, usually acute.

In *Allotropa virgata*, there are five broad distinct white sepals, "orbicular ovate to rhombic ovate, 4–6 cm. long, erose" (72).

In *Newberrya congesta*, the sepals are two brownish distinct, linear or nearly so (72).

In *Newberrya spicata*, the sepals are two, brownish-"spatulate, erose-fimbriate" (72).

In *Cheilotheca* there are 3–4 oblong lanceolate sepals (31).

In the Ericaceae, the sepals are usually green or brownish (exceptions to this occur as in *Cassiope hypnoides* with a red calyx), generally united, at least at the base. In *Kalmiella* and *Cladothamnus pyrolaeflorus*, the sepals are almost distinct. In a few the sepals are distinct as in *Epigaea repens*. All of the Pyrolaceae are similar in this characteristic to the Ericaceae—the sepals all being slightly united. In the Monotropaceae, *Pterospora* has a slightly united reddish brown calyx with narrow linear to lanceolate lobes. *Sarcodes* has a slightly united calyx, but the sepals are petalloid, crimson and large, almost as long as the corolla. In all of the other genera, the sepals are separate, 5–4–3 in number and petalloid, showing a gradual transition from small green united sepals in Ericaceae to large petalloid distinct ones in the most reduced members of the Monotropaceae.

In the Ericaceae, the sepals are often hairy, the hairs similar to those found in the Pyrolaceae and Monotropaceae. In *Cladothamnus campanulatus*, for instance, simple hairs like those of *Monotropa hypopitys* and stalked glandular hairs like those of *Pterospora* and *Sarcodes* occur.

The Petals

In *C. umbellata*, the petals are five, separate, concave, orbicular, pinkish in color, and 5–6 mm. in length. Under the microscope they show a fimbriolate margin that is ciliolate with numerous unicellular hairs.

In *C. maculata*, the petals are similar to those of *C. umbellata* except for the color, which is white.

In *P. rotundifolia*, there are five distinct, spreading, white, concave, roundish-obovate petals, about 7 mm. long with an entire margin.

Those of *P. elliptica* are similar except that they are greenish white in color and are about 6 mm. long.

In *P. secunda*, there are five oblong or elliptic erect petals, 4–5 mm. in length, greenish white in color.

In *P. minor*, there are five white or rose-colored, orbicular, concave, erect petals, 3–4 mm. in length.

In *P. chlorantha*, there are five greenish white, oval or elliptic, petals, 5–6 mm. in length.

In *P. aphylla*, there are five obovate petals, 6–8 mm. in length, whitish or tinged with brown or green on the outside.

In *Moneses uniflora*, the petals are five, occasionally six, concave, orbicular, white or pinkish, about 1 cm. in length, with a fimbriolate margin that is only visible under the microscope.

In *Monotropa hypopitys*, there are 5–4 yellow petals (five in the terminal flower, four in the lateral flowers). These are about 1 cm. in length and are narrow with a saccate base. Although the petals are not united, they are erect, with margins meeting, so that the flower appears campanulate. They are covered on the upper and lower surfaces with numerous simple, unicellular hairs.

In *M. uniflora*, there are five, occasionally six, white or pinkish petals that appear somewhat similar to those of *M. hypopitys*, except that they are larger (1.5 cm. in length) and thinner in texture, and only sparsely hairy on the inner surface, and entirely glabrous on the outer surface.

In *Sarcodes sanguinea*, the petals are five in number, united, campanulate (1–1.5 cm. in length), the five lobes are broad, rounded, and slightly spreading. No hairs are present on either surface.

In *Pterospora andromedea*, the corolla is urceolate, the five petals are white in color and united. They are 7–8 mm. in length, the lobes ovate to reniform, very short and recurved.

In *Pleuricospora fimbriolata*, there are five separate, slightly spreading, white petals, each narrowly oval, with a fimbriolate margin.

In *Schweinitzia odorata*, the corolla is pink in color. It is campanulate, with five lobes, which are ovate, shorter than the tube. The tube is 5-saccate at the base, as in Monotropa.

In *Allotropa virgata*, petals are absent.

In *Newberrya congesta*, the corolla is urceolate. The four lobes are ovate, about one-third as long as the tube which is pubescent within.

In *N. spicata*, the corolla is oblong campanulate, the four lobes oblong-ovate, about one-half as long as the tube which is pubescent within.

In *Cheilotheca* there are three erect, linear-oblong, yellow-red petals, 2.5 cm. in length.

In the Pyrolaceae, all of the species have five distinct petals. This is also true of the most primitive group of the Ericaceae, namely, the Rhododendroideae-Ledeae where *Elliottia* has four, *Tripetaleia* three, *Cladothamnus* five, *Bejaria* seven, and *Ledum* five petals. Distinct petals also occur in several members of the Monotropaceae, *i.e.*, *Monotropa hypopitys* with 5–4, *M. uniflora* 5–6, *Pleuricospora* 5–4, and *Cheilotheca* three. In other members of the Monotropaceae the petals are united. In *Pterospora*, the corolla is urceolate, resembling that of *Andromeda*. In *Sarcodes* and *Schweinitzia* it is campanulate, and in *Newberrya* urceolate to campanulate. Urceolate and campanulate corollas are quite characteristic of many of the Ericaceae. In the Ericaceae proper one can trace all transitions from a flat saucer-shaped corolla with separate petals, as in *Cladothamnus;* to shallow campanulate, as in *Loiseleuria procumbens;* to deep campanulate, *Epigaea;* to campanulate becoming slightly irregular bilobed, as in *Rhododendron;* to urceolate in *Andromeda* and *Vaccinium;* to deeply urceolate in *Erica* and *Thibaudia*. In the Monotropaceae, all these stages do not occur; there is quite a big gap between a corolla with distinct petals, as in *Monotropa*, and an urceolate one as in *Pterospora*, or campanulate as in *Sarcodes* and *Schweinitzia*. This would point to the view that perhaps these three arose from a higher group of the Ericaceae, and that the others arose from the Rhododendroideae-Ledeae with distinct petals. The very great similarity of these to each other (particularly *Sarcodes* and *Pterospora*, the writer having no good material of *Schweinitzia*) in all of their parts, and the rather great difference in structure between them and all other members of the Monotropaceae and Pyrolaceae give further evidence toward this view. In *Chimaphila* and *P. rotundifolia* and *P. elliptica* the corolla is slightly irregular—one petal extends downward so as to form a resting place for the insect. This parallels the condition in *Rhododendron* where the corolla is slightly bilabiate.

The presence of hairs on the inner surface of the petals seen in *Monotropa* is a characteristic of many members of the Ericaceae.

The Stamens

In all of the Pyrolaceae, the stamens, ten in number, are arranged in the bud so that the pores of the anthers point downward. When the flower opens, the anthers tilt backward, so

that the pores point upward. This is to insure pollination. Pollen grains occur in tetrads in all of the Pyrolaceae except *P. secunda*.

In *C. umbellata*, the filaments have two lobes toward the base. These bear numerous unicellular hairs along the margin. The anthers are violet in color and attached nearer the pore bearing end, and have two short horns opening by apical pores.

The stamens of *C. maculata* are similar to those of *C. umbellata* except that there are present on the margins of the lobes of the filament uniserrate hairs composed of 2–3 simple cells placed end on end. The anthers are attached near the middle.

In *P. rotundifolia* and *P. elliptica*, the filaments are not lobed and the horns on the anthers are very slightly developed.

In *P. secunda*, the anthers are oblong, opening by large pores. No horns are present. The pollen grains are single.

In *P. minor*, the anthers are not horned.

In *P. chlorantha*, the horns on the anthers are well developed, being about 0.5 mm. in length.

In *P. aphylla*, the horns are well developed, being about 1 mm. in length.

In *Moneses uniflora*, the filaments are awl-shaped, the anthers are prominently two-horned, the horns 0.5 mm. in length.

In *Allotropa virgata*, the stamens are described as having slender filaments, "anthers short, lobed, unappendaged, extrorse in the bud, introrse in anthesis, the sacs opening to near the middle by a chink." (72). This is the only member of the Monotropaceae that possesses the faculty of changing the position of the anthers in the opening bud, thus forming a connection between the Pyrolaceae and the Monotropaceae. Pollen grains are simple as in all the other members of the Monotropaceae.

In *Monotropa hypopitys*, the filaments are long, with unicellular hairs. They are pressed closely up against the ovary extending up to the stigmatic disk, the five opposite the petals being shorter than those opposite the sepals. The anthers are short, kidney-shaped, with transverse dehiscence, opening into two unequal valves.

The stamens of *M. uniflora* are similar to those of *M. hypopitys*.

In *Sarcodes sanguinea*, the filaments are long, slightly expanded at the base, extending up slightly further than half the length of the corolla, lying in the grooves of the ovary, and

bearing on their apices the rather long expanded anthers which open by two oval pores at the summit, turned toward the outside.

In *Pterospora*, the filaments are slender, the anthers short, each sac with an awn. The dehiscence is longitudinal.

In *Pleuricospora*, there are 10–8 stamens; the filaments are long and glabrous, the anthers long and narrow, opening by a longitudinal slit.

In *Schweinitzia odorata*, the anthers are short, opening by terminal pores.

In *Newberrya*, the stamens are 10–8 in number; the filaments are slender with long hairs. The anthers are oblong, erect on the tip of the filament, opening lengthwise.

In *Cheilotheca*, the anthers are erect on the filaments, and have longitudinal dehiscence (31).

In the Ericaceae, types of stamen similar to all those of the Pyrolaceae and Monotropaceae are present. Many of them have hairy filaments, as in *Chimaphila* and *Monotropa*. Simple oblong anthers occur as in *P. minor*, *P. secunda*, and *Sarcodes* with apical pores and not horned, *e. g.*, *Kalmia glauca* (12, p. 26, Fig. 17); others with exceedingly long tubes, as in *Vaccinium vitis-idaea* (12 Fig. 17) longer than in any of the Pyrolaceae and Monotropaceae. In the Pyrolaceae and Monotropaceae dehiscence of the anthers occurs in the same way as in the Ericaceae. Apical porous is quite common. Longitudinal dehiscence also occurs in practically all groups of the Ericaceae. In the Rhododendroideae-Ledeae, *Elliottia* and *Cladothamnus* have longitudinal, *Bejaria* and *Ledum* apical porous dehiscence. Transverse dehiscence occurs in the group Arbutoideae-Andromedae.

In the Ericaceae, the anthers may or may not be awned. In Figs. 17 and 18, p. 26, Drude (12) has figured *Erica tetralix*, *Arbutus unedo*, *Calluna vulgaris* with awned anthers, *Vaccinium vitis-idaea*, *Kalmia glauca*, *Rhododendron flavum*, and *Leiophyllum buxifolium* without awns. As a general rule the more primitive members of the Ericaceae with open flat expanded flowers do not have awned anthers, those with urceolate corollas generally do. This rule also applies to the Pyrolaceae and Monotropaceae; *Pterospora* the only member with awned anthers, has an urceolate corolla. The awns when touched by an insect tilt the anthers so that the pollen is dropped out on the insect's back.

The pollen grains of Ericaceae always occur in tetrads. This is true also of the Pyrolaceae except for *P. secunda*. This species forms a transition to the Monotropaceae where all the pollen grains are single.

The Pistil

In *C. umbellata*, the ovary is somewhat flattened-globose, with its outer surface ridged from the anthers being pressed up against it. The outer surface is covered with simple papillar hairs. It is completely five-celled, with a central placenta at the base, but the upper half is one-celled through the failure of the bilobed parietal placentae to meet and fuse in the center. The space between the placentae is, however, very small, so that it appears more like a five-celled ovary than a one-celled one. The placentae bear numerous anatropous ovules. The style is short, top-shaped. The stigma is broad and five-crenate, with a disc-shaped border. At the base of the ovary is a circular disc which secretes nectar.

In *C. maculata*, the ovary is similar to that of *C. umbellata*, the outer surface being ridged from the anthers, but no hairs are present. The number of cells, etc., is the same as in *C. umbellata*. The nectariferous disc is present, similar to that of *C. umbellata*. The style, however, is slightly longer; the five stigmatic lobes protrude slightly more from the disc.

In *P. rotundifolia*, the ovary is five-lobed, with glabrous outer walls. The same transition from a five- to a one-celled state occurs, as in *Chimaphila*, this being characteristic of the family. No nectariferous disc is present. The style is long declined, with the apex turned upward. The stigma consists of five narrow, erect lobes, which extend out from the top of the style that forms a rim beneath the stigmatic lobes.

In *P. elliptica*, the ovary and style are similar to those of *P. rotundifolia*. No nectariferous disc is present. The lobes of the stigma are however slightly longer, and the rim at the tip of the style greater in diameter than in *P. rotundifolia*.

In *P. secunda* the ovary is five-lobed, subglobose, with ten small nectariferous lobes at the base. The ovary is five-celled for most of the distance; the region where the placentae fail to meet is limited because of the deep insertion of the style. This is erect, straight, exserted, about 4 mm. in length. The stigma is peltate, much broader than the style, with five diverging lobes.

In *P. minor* there are no nectaries at the base of the five-lobed, incompletely 5-celled, ovary. The style is short, erect, 1 mm. in length, included in the petals.

In *P. chlorantha* the ovary is five-lobed, with 10 small nectariferous lobes at the base. The style is long, about 7 mm., exserted a little beyond the corolla, thickened upwards and declined as in *P. rotundifolia* and *P. elliptica*.

In *P. aphylla* the ovary is five-lobed with ten small nectariferous lobes at the base. The style is erect, short, 3 mm. in length.

In *Moneses uniflora* the ovary is ten-lobed. It is five-celled for the most part because the deep insertion of the style limits the region where the placentae fail to meet. No nectariferous lobes are present. The style is erect, inserted rather deeply into the ovary. It widens out toward the extremity forming a rim that is wider than that of *P. elliptica*, and with a stigma consisting of five fleshy lobes that are longer than in *P. elliptica*.

Fig. 8. Transverse section ovary *Pleuricospora fimbriolata* × 25.
1. Near base.
2. At middle.

In *Monotropa hypopitys* the ovary is ovoid, 10–8-lobed. As in the Pyrolaceae it is 5–4-celled at the base and one-celled above with 5–4 bilobed parietal placentae. At the base of the ovary there are 10–8 downward directed spur-like processes, which extend between the stamens and secrete nectar into the saccate bases of the petals. The style is thick and fleshy, longer than the ovary, it and the ovarian wall being strongly pubescent with unicellular hairs. Toward the top, the style

expands slightly, forming a ring, below this is a circle of hairs. The upper surface is hollowed out into a funnel-shaped 4–5-sided stigma.

In *M. uniflora* the ovary is ovoid, larger and more distinctly ten-lobed than in *M. hypopitys*. At the base are developed the ten nectaries similar to those of *M. hypopitys*, but larger. The style is shorter, the stigma much less hollowed out than in *M. hypopitys*, appearing more like a flat disc.

In *Sarcodes sanguinea* the ovary is smooth, ten-lobed, each lobe extending between two stamens and continued down into a nectar-secreting portion. It is five-celled at the base, becoming one-celled above as in *Monotropa*. The style is erect, bearing a five-lobed stigma.

In *Pterospora* the ovary is ten-lobed, depressed. It is five-celled below and one-celled above as in all the preceding. No nectaries are present. The style is short and broad, the stigma peltate-capitate, slightly five-lobed.

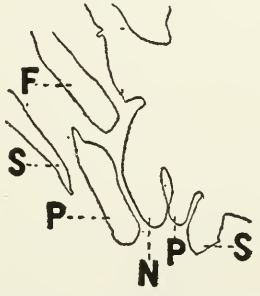

Fig. 9. Longitudinal section flower *Newberrya spicata* at base × 25. F = filament, N = nectary, P = petal, S = sepal.

In *Pleuricospora* the ovary is ovoid, not lobed, the epidermal cells bearing distinct pointed papillae. It is four-celled at the base (Fig. 8, 1) and for about one-sixth the length of the ovary, but further up (Fig. 8, 2) the four placentae fail to meet and do not extend far into the interior of the ovary, so that it appears as a one-celled ovary with parietal placentae. There are no nectaries present. The style is short and broad, the stigma depressed capitate.

In *Schweinitzia* the ovary is five-lobed with no downward directed nectaries at the base; it is five-lobed for about half the distance; the placentae do not extend in quite as far as in *Pyrola*.

The epidermal cells of the ovarian wall are slightly papillate. The style is short and thick, the stigma disc-like pentagonal.

In *Allotropa* the ovary is five-lobed. It too is five-celled at the base, one-celled above. There are ten small slightly down-directed nectaries at the base of the ovary.

In *Newberrya* the ovary is five-lobed, five-celled at the base, one-celled above. There are ten downward directed spur-like nectaries at the base of the ovary (Fig. 9). The ovary and style are pubescent with simple unicellular hairs. The stigma is depressed capitate.

In *Cheilotheca* the ovary is "fusiform, one-celled, narrowed into the short cylindric style; stigma globose conical; placentae six, parietal, bifid, the long branches on all sides covered by numerous ovules" (31).

In the Ericaceae a five-lobed, completely five-celled ovary is characteristic. In the Pyrolaceae and Monotropaceae there is every transition from a five-celled ovary with central placenta, as in the Ericaceae, to an incompletely five-celled ovary with the placentae deep parietal and almost meeting, as in all the Pyrolaceae, also *Sarcodes* and *Monotropa;* to an incompletely five-celled ovary with the placentae not so deep parietal, so that there is a good space between them, as in *Schweinitzia;* to *Pleuricospora* where the ovary is four-celled for only a short distance, then one-celled above with parietal placentae that are close to the ovary wall. Drude (12) states that all the Pleuricosporeae are one-celled. The writer finds the condition in *Newberrya* as in the Pyrolaceae; in *Pleuricospora* 4–1-celled as above; no material of *Cheilotheca* could be obtained for examination. Hooker (31) describes it as being one-celled with six parietal bifid placentae.

In Ericaceae the ovary is often covered with hairs, peltate glandular in *Rhododendron lapponicum;* glandular and setaceous in *Ledum palustre;* glandular in *Phyllodoce coerulea.* In the Pyrolaceae and Monotropaceae simple hairs are present in *Chimaphila umbellata*, in *Monotropa hypopitys;* and small papillae are present in *Schweinitzia odorata* and *Pleuricospora fimbriolata.*

The ovules in all three families are always anatropous. Correlated with the great numbers of ovules produced in the Pyrolaceae and Monotropaceae, is the rather remarkable number of pollen tubes developed from germinating pollen grains on the

stigma. These tubes pass down through the stylar canals and spread over the placental surfaces. They are most numerous in *M. uniflora*.

In practically all members of the Ericaceae there is at the base of the ovary a circular or crenately lobed nectary. In *Chimaphila* this is represented by a narrow collar-like rim. It is absent entirely in *P. rotundifolia*, *P. elliptica*, *P. minor*, *Moneses uniflora*, *Pterospora*, *Pleuricospora*. The disc or nectary is not continuous in any others of the Pyrolaceae or Monotropaceae, being represented by ten very small swellings in *P. secunda*, *P. chlorantha*, *P. aphylla*, and *Sarcodes sanguinea;* and by ten slightly larger and down directed lobes in *Allotropa*, *Schweinitzia*, *Newberrya*, and *Monotropa*.

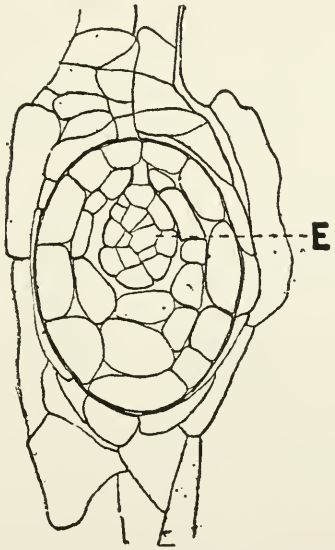

Fig. 10. Longitudinal section seed of *Pyrola rotundifolia* × 300.
E = embryo.

The Fruit and Seed

In the genus *Chimaphila*, the capsule is depressed-globose, five-valved, splitting from the apex downward. The valves are smooth along the edges. After the flower is pollinated, the pedicel straightens up so that the fruit is erect. This is true for the entire family. The seeds are small, numerous, and

consist of a thin cellular coat with an endosperm composed of a few large cells. The embryo has no form, but consists of several cells.

In the genus *Pyrola*, the capsule is five-lobed, splitting from the base upward. The valves are cobwebby on the edges, a distinction from the genus *Chimaphila*. The seeds in *P. rotundifolia* (Fig. 10) and *P. elliptica* are similar to those of *Chimaphila*.

In *Moneses uniflora*, the capsule is five-lobed, splitting from the base upward. The valves are smooth on the edges.

In *Monotropa hypopitys*, the capsules are oval, 5–4-celled, loculicidal. The seeds have a thin loose cellular covering; the endosperm consists of a very few large cells—much fewer and larger than in *Pyrola;* and the embryo itself is reduced to nine cells according to Koch (43), and five according to Solms-Laubach (74).

In *Monotropa uniflora*, the capsule is ovoid, dehiscence as in *M. hypopitys*. The seeds are similar to those of *M. hypopitys* in the number of endosperm cells, but appear to be even more reduced in the number of cells in the embryo, the writer's material showing only two.

In *Sarcodes*, the capsule is spheroidal, 9–21 mm. broad, with circumscissile dehiscence, the line of dehiscence 1–1.5 mm. below the base of the style. Oliver has described and figured the seeds of this. In regard to the amount of endosperm and number of cells in the embryo he states that it is very similar to that of *M. hypopitys*.

In *Pterospora*, the capsule is five-lobed, five-celled, loculicidal, the valves cohering with the columella. The seeds are very numerous, ovoid, and are broadly winged at the apex (Drude (12), p. 10, Fig. 6–K).

In *Pleuricospora*, the capsule is ovoid, one-celled.

In *Schweinitzia*, the capsule is ovoid, five-celled, seeds numerous.

In *Allotropa*, the capsule is "spheroidal, 4–5 mm. broad" (72). In seeds examined by the writer, the endosperm shows the same number of cells as in *Monotropa*.

In *Newberrya*, the capsule is short, usually ovoid. The writer had no ripe capsules, but found the ovary five-celled, so concludes that the capsule is five-celled also.

In Ericaceae, the fruit is a capsule, with septicidal or loculicidal dehiscence, or a berry. In the Pyrolaceae and Monotropaceae the fruit is a capsule, as in the primitive Ericaceae. It is characteristic of many Ericaceae, *e.g.*, *Cassiope hypnoides*, *C. tetragona*, *Phyllodoce coerulea*, that after flowering (in species with drooping flowers) the pedicels straighten out so that the fruit becomes erect. This is characteristic of all of the Pyrolaceae and Monotropaceae.

In typical Ericaceae, the seeds are small, the largest 1–2 mm. The endosperm is well developed, the embryo distinctly formed, a root and two cotyledons always present. In the Pyrolaceae and Monotropaceae the seeds are smaller and more numerous. In structure they are much reduced. The endosperm in the Pyrolaceae consists of relatively few large cells—the embryo of about 25–30 cells with no trace of cotyledons. In the Monotropaceae the number of endosperm cells is still less and the cells are larger, the embryo also is very small, composed of only nine or five cells (43, 74).

Summary

In the Ericaceae the plants are shrubby or sub-shrubby. The Pyrolaceae show a gradual reduction from sub-shrubby in *Chimaphila* to herbaceous in *Moneses*. The Monotropaceae are entirely herbaceous. The underground rhizome, producing adventitious buds and roots, in many of the Ericaceae, in *Chimaphila* and *Pyrola*, gradually has its function of producing buds and roots taken over by the root which becomes long and horizontal in *Moneses*, becoming condensed to short and fleshy in the Monotropaceae. There is a gradual increase in the amount of hyphal investment in the roots from *Chimaphila* through *Pyrola* to *Monotropa*, the most saprophytic, correlated with a gradual decrease in the number of layers in the root cap. In the structure of the ascending axis, there is a gradual decrease in the amount of wood formed, from typical Ericaceae, with very woody stems through *Chimaphila* which is as woody as some of the smaller Ericaceae, through *Pyrola* and *Moneses* which are less woody, to the Monotropaceae, reaching its climax in *Monotropa* where the amount of wood is very limited. Correlated with this is a gradual increase in the amount of phloem. There is a gradual reduction in the size and structure of the

leaves from evergreen leathery in Ericaceae, *Chimaphila*, and some of the Pyrolas, to less leathery in *P. chlorantha* and *P. minor*, to evergreen leaves but with deciduous structure in *Moneses*, to scales which are brownish (*Pterospora*), brownish yellow or yellow (*M. hypopitys*), red (*Sarcodes*), brownish white (*Pleuricospora*), to white (*M. uniflora*). This is correlated with the gradual increase in size and persistence of the scales from green or brownish in the Ericaceae to herbaceous, persistent, but still small in the Pyrolaceae, to large fleshy and colored in the Monotropaceae. Stomata are very numerous on the leaves in the Ericaceae, become less numerous in the Pyrolaceae, very few in the scales of *Monotropa* and *Pterospora* and absent entirely in those of *Sarcodes*. All of these changes are correlated with increasing saprophytism.

The inflorescence is a raceme or condensed to a corymb, or solitary in each of the three families. The sepals are green, united, in the Ericaceae and Pyrolaceae; brownish, united, in *Pterospora;* red, very slightly united, in *Sarcodes;* becoming separate, yellow, in *M. hypopitys;* and white in *M. uniflora.* The petals are 5–4, separate, to united shallow campanulate, to campanulate, to irregular campanulate, to urceolate in the Ericaceae; there are five separate expanded, to separate campanulate in the Pyrolaceae; to separate campanulate in *Monotropa;* to united campanulate in *Sarcodes;* to urceolate in *Pterospora.* Stamens are generally twice the number of petals in the Ericaceae, and always so in the Pyrolaceae and the Monotropaceae. They bear two horns in many of the Ericaceae and Pyrolaceae. They are awned in the urceolate corolla types in the Ericaceae and in *Pterospora* (which has an urceolate corolla) of the Monotropaceae. The dehiscence is apical porous, longitudinal, or transverse in the Ericaceae, apical porous in the Pyrolaceae; and apical porous, longitudinal, or transverse in the Monotropaceae. Pollen grains occur in tetrads in all of the Ericaceae and all of the Pyrolaceae except *P. secunda.* In *P. secunda* and all of the Monotropaceae they are simple.

In the Ericaceae, the ovary is completely 5–4-celled. In the Pyrolaceae, in the upper half of the ovary the placentae fail to meet and fuse. They almost meet, so that the ovary is practically five-celled. In the Monotropaceae, there is a gradual decrease in the length of the placental in-growths to *Pleuri-*

cospora where the placentae are placed close against the walls and the ovary is practically one-celled. At the base, however, even in this most simplified form, the ovary is four-celled. At the base of the ovary in practically all of the Ericaceae, there is a nectariferous disc. This is represented either as a collar-like rim in *Chimaphila*, or ten very small swellings as in *P. secunda*, *P. chlorantha*, *P. aphylla*, and *Sarcodes* or ten downward directed nectaries in *Allotropa*, *Schweinitzia*, *Newberrya*, and *Monotropa*. The ovules in all three families are anatropous. In the Ericaceae, the seeds are small with abundant endosperm and a well-formed embryo; reduced in size but increased in number in the Pyrolaceae with a less developed endosperm with larger and fewer cells, and a formless embryo composed of about 25–30 cells; still further reduced and more numerous in the Monotropaceae with an endosperm consisting of a few large cells and a very small embryo composed of 9–5 cells. The change in the ovary from five-celled with central placentae to one-celled (nearly so in Pleuricospora) with parietal placentae; and the increase in number of seeds and reduction in number of cells of the endosperm and embryo are all evidence of increasing saprophytism.

Conclusions

From the preceding summary, it is seen that all of the supposed differences between the Ericaceae and the Pyrolaceae are broken down, except that the ovary is completely five-celled in the Ericaceae, and incompletely five-celled in the Pyrolaceae. The distinction is so slight that it seems unreasonable to use it as a basis for separating the two families. The only distinction that holds between the Pyrolaceae and the Monotropaceae is the absence of green coloring matter in the latter. In *M. hypopitys*, small grains are present in the epidermis of the scales. These are probably chromoplasts which develop from chloroplasts by degeneration.

The Pyrolaceae and Monotropaceae therefore differ from the Ericaceae only in their gradually increasing saprophytism and in those characters which go hand in hand with this, *i.e.*, the loss of green coloring matter, the reduction from shrubs to herbs, reduction of leaves to scales, the ovary from five-celled with central placentae to almost completely one-celled

with parietal placentae, the increase in the number of seeds and the reduction in their size and in the number of cells of the endosperm and embryo. The writer has traced such a gradual transition in structure from the simplest group of the Ericaceae, *i.e.*, the Rhododendroideae-Ledeae, through the slightly saprophytic Pyrolaceae to the completely saprophytic Monotropaceae. The genera *Pterospora* and *Sarcodes* seem in their characters to be different from the others, as if these two had arisen in a different line, perhaps from some of the higher members of the Ericaceae with campanulate or urceolate corollas.

On account of the lack of distinct differences and the numerous resemblances and intergrading characters between the more primitive Ericaceae, the Pyrolaceae, and the Monotropaceae, the writer concludes that the last two should be considered as sub-families under the Ericaceae.

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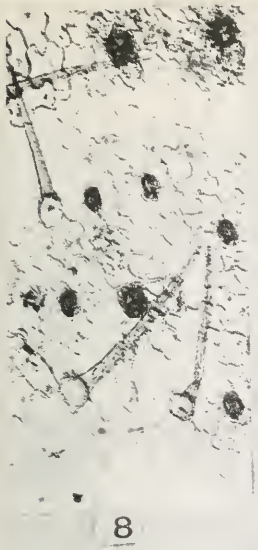
RUSSELL ON SARRACENIA.



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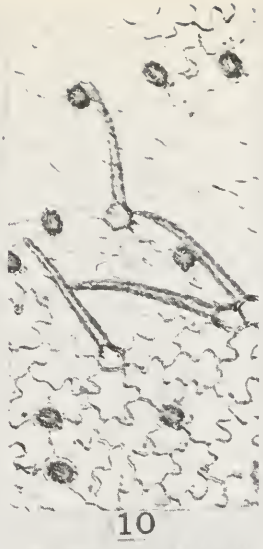

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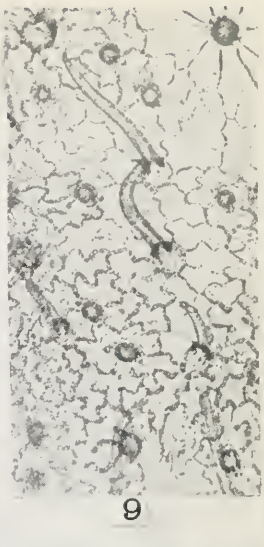

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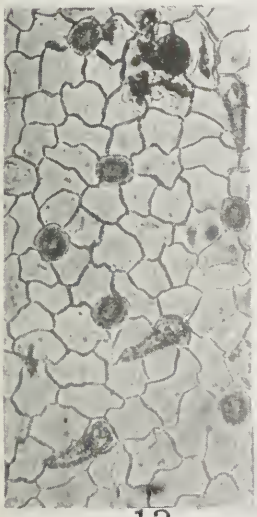

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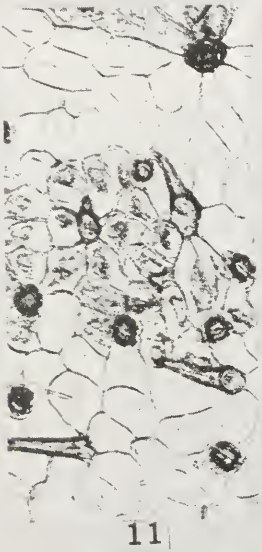

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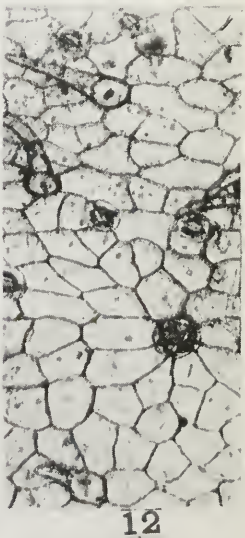

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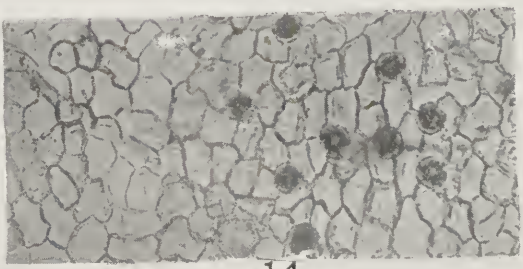

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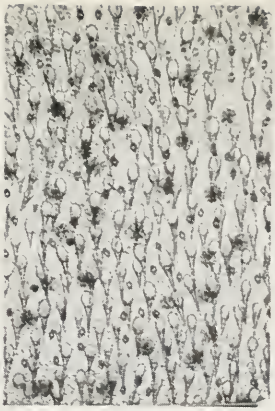

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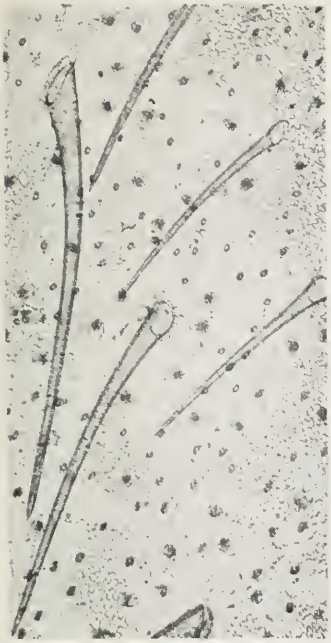

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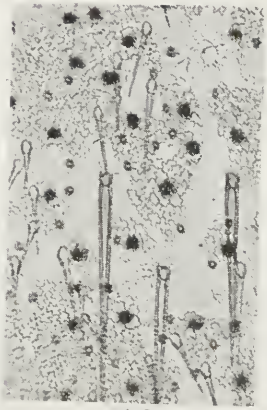

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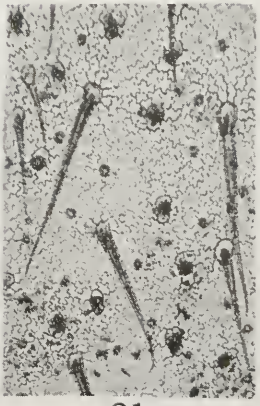

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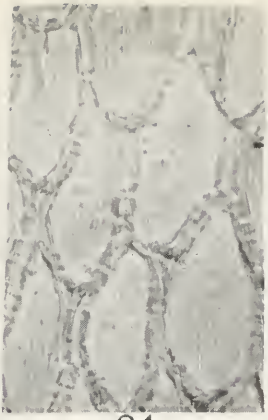

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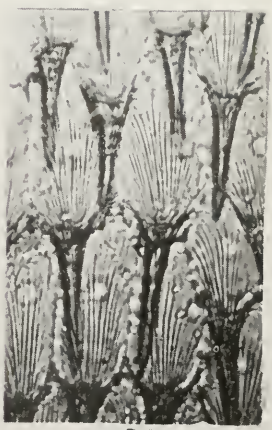

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1920

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A MORPHOLOGICAL AND CYTOLOGICAL STUDY OF REPRODUCTION IN THE GENUS ACER

By William Randolph Taylor, B.S., M.S.

With Plates VI–XI.

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Introduction

At the inception of this work the writer planned to review the genus *Acer* from the standpoint of the evolutionary tendencies shown by the comparative morphology of the floral parts, as well as the relative degrees of diœcism and flowering periods of the different species. A preliminary survey of the available sources of material and information showed that it would be impracticable to secure sufficient data to insure a comprehensive view of all of the sub-genera. This was especially true with respect to living material. On the other hand, the literature regarding the development of the reproductive elements was found to be very meagre, and in some particulars, contradictory. Since as many species as could be handled in a cytological study were within reach, an attempt to clear up the points in dispute and to extend our knowledge of the genus to unstudied species led to the abandonment of the original problem.

Historical

The first paper to appear dealing with the cytology of *Acer* was by Ira D. Cardiff in 1906 (2). This was primarily a study of synapsis and the organization of the heterotypic chromosomes, presenting the viewpoint of parallel pre-synaptic threads and paired chromomeres. He worked with *Acer platanoides* and several other plants of widely differing groups, describing an essential similarity of behavior throughout. The reduced chromosome number for the maple considered is given as eleven.

This work was followed by a study of *Acer negundo* by Chester A. Darling in 1909 (4), an effort to determine the basis for the diœcious condition in this form. The whole history of the maturation divisions as described by this author is at variance with the usual process of pollen development. The chromatin is said to leave the nucleolus during the presynaptic phases in the form of round bodies which build up the spireme on the linin threads. Later the spireme breaks up to form eight bivalent chromosome segments, while from the nucleolus bud off directly five more bivalents. Upon the breakdown of the nuclear membrane what is left of the nucleolus is said to divide up into a few granules which pass out from the spindle region.

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The thirteen chromosomes thus formed divide equally and there is found no basis in an unequal division for a differentiation into male or female determining individuals. But Darling considers that in the reorganization of the nuclei in the tetrad two of the nuclei contain each a chromatin body lacking in the other two, and that this feature may be related to sex determination. The body in question seems to disappear soon after, during the passage into the resting state.

The unusual conditions represented by this author as present in *Acer negundo* were denied in a subsequent work by D. M. Mottier on the same species, published in 1914 (13). Here a very clear and convincing account is given of the conditions present and a comparison made with the somewhat related *Staphylea trifolia* L. He also, besides giving a more normal history as that typical of the maple, disputes the correctness of the count, giving twelve as the probable number in one place, and in another suggesting either twelve or fourteen. Mottier incidentally gives the chromosome count in *Acer rubrum* as thirty-six in the reduced condition. In an earlier paper (12) he describes the mature pollen of this species.

With regard to the ovule development, the only paper available is that of Mottier on *Acer rubrum*, 1893 (12). He reports that late in March the megaspore mother-cell is evident as a sub-epidermal cell, which becomes more deeply placed by later divisions of the nucellar epidermis. Its first appearance was not determined. The first division in the mother-cell is followed by wall formation, and then the more micropylar of these again divides with a resulting wall. Both these cells degenerate. The more chalazal of the original pair divides later than the other, but no wall is laid down, and the embryosac by two additional successive divisions reaches the eight-nucleate stage. The three antipodals early disappear after maturity, and the polar nuclei fuse preliminary to fertilization.

Material and Methods

The writer was fortunate in being able to obtain material of a considerable number of species, both native and exotic in origin. The greater part of the exotic material could not be worked up with thoroughness, and so will not be considered in this paper. Buds of *Acer platanoides* L. and *Acer rubrum* L. were made avail-

able early in the spring of 1918 by forcing in the greenhouses. These were again collected at the normal flowering season, with, in addition, *Acer pseudo-platanus* L. Little was done with the less common introduced species until the next season, when a considerable series was obtained, as well as *Acer negundo* L. buds, and the root tips of some species for vegetative mitoses. In all, about two hundred fixations were made. The material was found to be extremely hard to fix properly, a tendency being evident for the chromosomes to clump at metaphase, which caused many fixations to be discarded. The solution finally adopted was a Strong Flemming containing less than one per cent. of Urea and Maltose. The bud scales were first dissected away and the flower mass plunged beneath the surface of alcohol for a moment to drive the air from the interstices, from which it was removed to the fixing solution. The large inflorescences were separated into several parts to facilitate penetration. Some species have resinous bud scales or tufts of hairs between the flowers which render it almost impossible to get satisfactory results. Later stages in the development of the ovules necessitated the cutting away of the ovarian walls. Except in the case of *Acer pseudo-platanus*, the root-tips used were obtained from greenhouse cultures. They were fixed in Weak Flemming. For pollen and vegetative cell studies sections were cut 4–5 microns thick, and for embryosac and embryo studies appropriate to the stages represented. The stain used throughout the cytological part of the work was Heidenhain's Haematoxylin.

The writer is much indebted to the many friends who have by contributions of living material or otherwise, assisted in this work. To Dr. John M. Macfarlane acknowledgement is made of the original suggestion and for the complete facilities under which the work was conducted. For a large part of the fresh material of *Acer rubrum* L., as well as other items, he must thank Dr. Alice M. Russell. Through the kindness of Mr. Roberts LeBoutillier the writer was able to collect much material from Japanese species growing on his estate. Prof. C. S. Sargent very generously sent a considerable number of species from the Arnold Arboretum, but as the flowers in this material were largely open, they will not enter into the present paper to any great extent.

Floral Development

The maples fall into two classes with respect to their time of flowering, the one blooming before the development of the leaves, the other after they have begun to expand. This fact has been recognized in the subdivision of the genus (14). In the region of Philadelphia *Acer saccharinum* and *Acer rubrum* bloom within about ten days of each other, in late February or early March. Then there is a period of ten days or more before any other forms appear. These first two both flower before the leaves appear, and so also does *Acer negundo*, which ushers in the most active blooming period. A few of the exotic species only, seem with us to delay beyond the latter part of April.

The early blooming of the three forms named, correlated as it is with a reduced perianth and marked diœcism, would lead one to suspect a possible difference from other species in the period of pollen maturation and other reproductive phenomena. Only one of these, however, shows such a condition. *Acer saccharinum*, which flowers earliest in the spring, matures its pollen in the autumn. The writer followed the development of the flower buds closely during September and October, 1919, and found that development was very gradual till the time for the reduction divisions came near. Then a rapid growth in size accompanied the divisions. This phase came about October 20–24. The period of the formation of the tube and generative nuclei appears to be in late winter, generally during early February (Fig. 27). Flowering occurs from the latter part of January, by the earliest records available, to the middle of March in exceptionally late seasons and sporadic cases. The great majority of the trees flower together during the first thoroughly warm spell of the year.

This species is followed by *Acer rubrum*, generally during the early part of March, though, exceptionally, earlier. Here pollen maturation does not take place in the fall, but during the opening of the flower buds. The reduction divisions take place during the swelling of the bud, and the tetrad stage is reached as the anthers appear between the scales at the tip. The formation of the tube and generative nuclei occurs just before the rapid elongation of the filaments which accompanies anthesis. The sperm nuclei were not seen: they are formed probably subsequent to the shedding of the pollen.

Acer negundo follows a week or ten days later than *Acer rubrum*, and maturation of the pollen also occurs during the opening of the buds. In these three forms, with relatively condensed inflorescences it might be expected that in any given bud the stages would be almost simultaneous, but a great variation, even in the lobes of a single anther, was the regular condition. The same holds true for *Acer saccharum*, which blooms a little later than *Acer negundo*.

It is, however, in the forms with a more complex inflorescence that this variation in the time of development reaches the greatest degree. *Acer platanoides*, the next of the common forms to open, will show any condition from mature archesporium to young pollen grains in the same flower cluster. This renders the accumulation of a considerable quantity of material of any one stage rather a prolonged task. Maturation occurs during the swelling of the bud, and by the time the scales have opened, most of the anthers will contain pollen grains. The time for the actual flowering of this species is generally the second week in April. *Acer pseudo-platanus* has the largest flower mass of any of the commonly grown species, and here development proceeds from the base of the raceme toward the tip, with great secondary differences in the stage of development of the flowers on the secondary racemes. The reduction divisions take place largely while the racemes are from 10–15 mm. in length. It flowers soon after *Acer platanoides*. Data for the Japanese and the more rarely cultivated European species are incomplete, but they mostly flower, in this region, during April or early May.

It proved much more difficult to get information with regard to the time at which the reduction divisions take place in the megaspore mother cell. In general it was found that in a flower with young microspore tetrads, the megaspore first prophases were taking place, while the later phases followed the separation of the tetrad.

Abnormalities in floral structure were not especially sought, but some few appeared. With regard to the constancy of the diœcious condition in *Acer saccharinum* and *Acer rubrum* it should be noted that trees of both species bearing alike male and female flowers were found. The flowers occurred in different inflorescences on the same twig in *Acer saccharinum*. Predominately male clusters of *Acer platanoides* often bore a few

flowers, opening later than the others, in which the ovaries were normal in appearance.

Details of abnormalities in the structure of individual flowers were not noted, except the occurrence of tri-carpellary ovaries. These were found in *Acer rubrum*, *Acer saccharinum*, *Acer saccharum*, *Acer platanoides*, and *Acer pseudo-platanus*, the forms in which quantities of female material underwent close examination.

Pollen Development in Acer Negundo

The early stages in the development of the anther and the origin of the tapetum and archesporium were not traced. There was some variation between the different species in the number of layers forming the wall. An epidermal layer, and an outermost endothecial layer of larger cells were always present. In addition inner wall layers were found, varying in number from one which disorganized at maturity in *Acer spicatum* Lam. to three, of which one persisted in the mature anther, in *Acer pseudo-platanus*. The tapetum was always strikingly developed. It was found to show a multinucleate condition of the cells in all of the forms studied, and the nuclear divisions giving rise to this state occurred both by a somewhat abnormal looking mitosis and by amitotic fission. The latter was by far the commonest, and the daughter nuclei often remained attached to each other, forming a cluster near the center of the cell. Both began about the time of synapsis, and in the mitotic type the number of chromosomes appeared in excess of the normal sporophytic number (Figs. 31–33).

The material at hand has permitted a fairly complete study of five species with regard to the details of the reduction divisions in pollen formation. These are *Acer negundo*, *Acer rubrum*, *Acer platanoides*, *Acer pseudo-platanus* and *Acer saccharum*, in addition to which fragmentary material of several other forms was available. Of these, by far the best quality of material came from the first named. The low number of chromosomes in this species makes it a very satisfactory one for study, and since the writer found some differences of detail from the description given by Mottier (13) a synopsis of the stages in *Acer negundo* will precede a comparison with the other forms studied.

With the growth of the archesporial cell after the last vegetative division, the chromatic material becomes largely confined to the nucleolus and only a delicate peripheral linin network marked by a few chromatic granules can be distinguished (Fig. 1). With the approaching heterotypic prophase the number and size of these granules increase, but there is no sign of the paired condition of threads and granules described by Cardiff (2). As the leptonema network becomes strongly defined the irregularity decreases somewhat, and it passes into synapsis in the form of a net, not as a continuous spireme thread (Fig. 3). The actuality of synapsis as a condition in the living cell has been much questioned, especially by the animal cytologists (11), but it is a constant feature in the present material (Fig. 4). One thing seems sure, however: the more evidence there is of poor fixation, the more the synaptic knot appears as a structureless black mass, and the less as an aggregation of threads. It is quite conceivable that still further refinement of technic would eliminate it, with consequent abandoning of its emphasis as an explanation of various phenomena of inheritance, but the maples are so resistant in the walls of their rather small anthers to the penetration of fixing fluids that they would form poor material on which to base a critical series of experiments.

From synapsis the spireme emerges in the form of loops (Figs. 5, 6), which extend to the periphery and result in a very distinct hollow spireme (Fig. 7). The figures in this paper differ from those given by Mottier in the greater delicacy and complexity of the thread system, especially at the hollow spireme stage. It is probable that this is due to a difference in fixation, and the writer feels that the condition here figured is the more representative. There is good evidence of anastomosis between the strands at this stage, and the longitudinal split present in some plants could not be distinguished.

As shortening of the system during the approach of strepsinema proceeds, it becomes evident that the thick bands that are to form the chromosome pairs are formed by the lateral approximation of threads (Figs. 8, 9, 10). This opens up the controversial question of the nature of the spireme, which has recently been admirably presented by E. Digby (6). In a general presentation such as this it seems well to withhold a discussion of the matter, acknowledging, however, its important bearing on current theories.

There is no spiral twisting of the paired threads such as is so characteristic of the stage in the lily (Fig. 11). Instead, they break up into a number of segments equal to the reduced chromosome count. These may appear to collect somewhat to one side of the nucleus in a second contraction, but the writer is rather inclined to believe that this appearance is in the nature of an artifact. The halves of each pair now separate more or less, forming very conspicuous rings (Figs. 12, 13), which by separation at the ends and contraction give rise to the chromosome pairs, seeming to pass through a twisted stage during the shortening. Finally all elements contract to very short rods closely associated in pairs lying around the periphery of the nucleus (Fig. 14). The number of these is readily counted when few, as in this case, but in those forms with many chromosomes, as described later, the task becomes much more difficult.

The nucleolus has from the earliest beginnings of the division kept its large size and quality of strongly retaining the stain. Although for the most part apparently connected by strands with the spireme, the writer would not consider that it contributed chromatin material by bodily transfer, as has been suggested (4), but rather through the intermediary of products dissolved in the plasma and which are recombined in the spireme into stainable chromatin. This is not an hypothesis readily capable of demonstration, but it fits the observed conditions better than the other.

With the approach of diakinesis as described, there appears gradually a denser interior cytoplasmic zone surrounding the nucleus, which eventually resolves itself into a complex system of filaments that show signs of aggregation into sheaves by the time the breakdown of the nuclear membrane occurs. At this time the cytoplasm rapidly encroaches on the nuclear cavity, strands pass into it, and the chromosomes become forced toward the center (Fig. 14). The filaments then rapidly swing around into a few sheaves showing as a multipolar spindle, and then into two in the typical fashion. All this while the nucleolus has been rapidly decreasing in size so by the time the bipolar condition has been reached, the nucleolus has disappeared (Figs. 17, 18). The chromosome pairs then become arranged in the nuclear plate, the small rounded elements of each pair being directed toward the poles, not lying side by side in the plane

of the equator (Fig. 15). This fact is of importance in connection with making the chromosome counts, for in a precise polar view it eliminates the likelihood of confusing the count through inclusion of both elements of a pair, since the member above completely covers and hides from view its homolog below.

During anaphase the chromosomes pass to the poles as small, more or less ovoid bodies (Fig. 16). They are figured by Mottier as being elongate, and during the late anaphase as showing the split that so frequently is to be observed in plant chromosomes at this stage. In the writer's material, the better fixed the material appeared, (as judged by lack of shrinkage and especially by the wide and even distribution of the chromosomes in the plate), the less the chromosomes appeared elongated in the anaphase condition. The only elongation that was seen appeared to be due to a tendency of some of the chromosomes to stick together, probably a fault of fixation, and this increased greatly in material in which clumping of the chromosomes was present. As for the split, that could not be distinguished by the writer in any of the species he examined. It is to be noted that these bodies are extremely small: from one-half to one micron only in diameter, and the writer has been unable after long observation to find evidence of bipartition.

A count of the reduced number at metaphase or early anaphase is readily made in such a species as *Acer negundo*, which fixes well and has a small number of chromosomes. This is for the present case given by Darling (4) as thirteen, but in the later paper by Mottier (13) this is questioned, twelve being stated as the probable number, with, elsewhere, fourteen as an alternative. Why the intermediate count of thirteen should be discarded when the investigator seems in doubt whether the number just above or just below that first given is more correct, the present writer fails to see, since there is no especial reason to expect an even number for the reduced count. The material available for the present paper gave ample clear counts of thirteen to establish this number as the gametophyte chromosome count (Figs. 51–56 incl.).

When the chromosomes approach the poles, they tend to spread out as flattened structures and to anastomose by projections from their edges (Fig. 20). This forms a bowl-shaped structure open on the side facing the equator of the spindle

(Fig. 19). The open space is filled with a clearer and less vacuolate plasma than the general neighboring region, clearly differentiated from the spindle which it terminates. The nuclear membrane first becomes evident over the external face of the bowl, gradually extending around the sides and contracting the open face, accompanied by the chromatin which becomes distributed over the entire periphery by the time the membrane is complete. The reticulum then rapidly loses its definiteness, but it does not seem to pass through a series of comminuting stages that are in effect a reversal of the prophase stages. The nucleolus in its earliest appearance is difficult to distinguish from the large chromosome-derived bodies, but these stain more lightly and become smaller the later the stage studied, while the nucleolus gradually becoming larger, can soon be recognized (Fig. 21). This nucleolus in many cases seems to be the only chromatic body at interkinesis, but deep staining shows that there remain angular structures on the periphery about equal in number to the chromosomes that went into the nucleus (Fig. 22).

The second or homotypic prophase begins with the establishment of dark-staining angular bodies on the nuclear periphery, seemingly from the centers just mentioned (Fig. 23). As these increase in size the nucleolus shrinks, retaining its dark staining capacity. They can often be counted, but the contour of the nucleus and its small size reduces greatly the number of favorable countable cases. After the break-down of the membrane (Fig. 24) they pass from an irregular distribution into the flat plate preparatory to division. The nucleolus, still present, passes out from the forming spindle and takes up its position where the apex of the heterotype spindle had formerly been (Fig. 25). It retains its staining capacity up to this point, and is a very conspicuous object. The equatorial part of the heterotype spindle remains distinct through the homotype division (Fig. 26). The nucleolus disappears suddenly, shrinking and paling without evidence of fragmentation.

The axes of the two homotype spindles may lie in the same plane, or in two planes at right angles to each other, or even in any intermediate position, thus giving rise to tripartite or cruciate tetrads, or intermediate forms.

After separation of the tetrad the elements enlarge considerably, and each forms its individual wall that, as the pollen grain

nears maturity, shows three thin lines which after shedding permit the emergence of the pollen tube. The mature pollen grain has but two nuclei, the tube and generative nuclei, and the latter remains undivided till after the pollen grain has been shed. The appearance of the pollen grains of the various species is similar, size being the only evident difference (Fig. 27). The pollen grains of anthers in female flowers more often showed abnormalities than in anthers of male flowers, and showed degeneration as anthesis approached.

Pollen and Somatic Divisions in Other Species

The history of pollen development as given for *Acer negundo* is typical in a general way of the genus. The differences observed in other forms are for the most part those necessary to effect the distribution of the larger number of chromosomes.

Amitosis was the most common form of nuclear division in the tapetum cells, but mitotic division was observed in other forms than *Acer negundo*, notably *Acer pseudo-platanus*. There was no special differentiation of the cytoplasm near the spindle in *Acer negundo*, but in *Acer saccharum* and *Acer platanoides* a denser zone was present, slightly removed from the spindle and surrounding it. In *Acer rubrum* such a dense area was present in a pronounced form, frequently assuming a unilateral or unipolar position (Figs. 29, 30). This appearance is hardly likely to be an artifact, for the general fixation of the cytoplasm and of the chromatin is quite good. In the forms with high chromosome numbers there was naturally a greatly increased complexity of the spireme at all stages, and especially was this true of *Acer rubrum*. A complete discussion of certain peculiarities of this form are given later, but it is best mentioned here that as strepsinema approaches there appears a much more decided twisting of the spireme than was found in *Acer negundo* (Fig. 28). This was true to some extent of the other forms. The extreme complexity of the spireme mass prevented a complete study of *Acer rubrum*. Certain material of this species showed a great deal of abnormality in the pollen grains, described later, and in addition to these structural variations in some cases delayed division of the nucleus into tube and generative nuclei. Division of the generative nucleus within the grain was not observed, either as a normal or as an abnormal occurrence.

In *Acer platanoides* the reduced number of chromosomes is given by Cardiff (2) as eleven. This the writer has been able to confirm, although the amount of material available was not great (Figs. 59–62). The seeds of this species were germinated and the root tips fixed to verify this by making a 2x count. Here a word must be recorded with regard to the conditions of observation of the mitoses, especially the somatic ones. In all of the maples studied the chromosomes in the vegetative parts are very small indeed. The longest studied measures about three microns in length and the smallest about one micron, with in both cases a diameter of from two-thirds to one-third micron. Even with good fixation, which with the roots was consistently obtained, overlapping of the ends of these bodies, and other confusing arrangements frequently occurred. This made the interpretation of the complex plates a difficult matter, and in the extreme cases of *Acer rubrum* and an abnormality under *Acer saccharinum*, compels the count arrived at to be considered merely as a very careful approximation. The method pursued in making all the chromosome counts, both somatic and gametophytic, was to draw the most perfect plates with the camera lucida at a magnification of 3380 diameters, correct the rough sketch by direct observation and recompare under the camera before counting. This enabled the writer to be sure no element had passed by unobserved. In the cases of small 1x plates, a few actual drawings were supported by many direct observations, readily made when a small number of elements was concerned. With *Acer platanoides*, having the smallest number of chromosomes yet observed in the genus, it was a surprise to find that the somatic count obtained in the root tip cells did not agree with the reduced count, for the number twenty-six was persistently obtained (Figs. 57, 58). A very few counts of twenty-five, twenty-seven and twenty-eight probably contain observational errors. The difference between the observed number and that of twenty-two which was expected, is too great to be an error, and indicates probably that there exist varieties differing in cytological composition. As no systematic attempt was made to keep records of the exact trees furnishing the material for each fixation, these features unfortunately cannot be correlated with the horticultural forms and varieties listed by Pax (14). A further feature of this kind appeared and will be considered under *Acer rubrum*.

Acer pseudo-platanus was studied with respect to both the vegetative and reduced counts, with the result that twenty-six and fifty-two were found to be the 1x and 2x numbers. The root-tips of this species furnished especially favorable material for counting, and no significant variations appeared (Figs. 63–66).

The Sugar Maple, *Acer saccharum*, showed few and large chromosomes, thirteen being the observed 1x number (Figs. 69–71).

Only one of the remarkable oriental maples, *Acer carpinifolium*, will be noted here. This has, as the name indicates, leaves resembling the Hornbeam, *Carpinus*. This condition made it of interest to obtain a count, and the results indicate that fifty-two is the probable somatic number in this case, as in the last (Figs. 67, 68). The group was not shown to be strikingly different cytologically, therefore, from the forms with lobed leaves.

Because the rapidity with which the pollen maturation of the Silver Maple occurred in the fall was unexpected, the writer failed to obtain reduction division material that would furnish the 1x count. In a pollen grain a countable anaphase polar view was however obtained, the two plates giving in one case a clear twenty-six and in the other a more uncertain twenty-seven as the chromosome number (Fig. 73). Germination of the seeds gave material for the 2x count, which was determined to be between fifty-one and fifty-five, in all probability fifty-two as in the preceding cases (Figs. 72, 75). The plates and the individual chromosomes of this species are the smallest observed, if the number involved is considered. In two roots of this form, *Acer saccharinum*, cases were found where the chromosome number, while too great to be exactly determined, approximated a 4x condition at metaphase (Fig. 74). Most of the plates in these roots were of the normal type, indicating that this was an individual cell variation, probably by lack of separation of the daughter groups at the metaphase of a former division. A condition believed to be similar, but not so clear, was observed in the pedicels of *Acer negundo*.

The most perplexing situation presented, however, is that of the Red Maple, *Acer rubrum*. There is but one reference to the cytology of this form, a sentence in Mottier's paper on *Acer*

negundo. He there gives the reduced chromosome count for *Acer rubrum* as thirty-six, the same as *Staphylea*. This marked the form as strikingly different in nuclear composition from the others then known, *Acer negundo* and *Acer platanoides*. It was early examined by the writer for comparison with the others, but the number of chromosomes was so large that with the poor fixation at first obtained, it seemed impossible to obtain a count. With later material better success was attained, and the number determined as being between sixty-eight and seventy-five (Figs. 30, 79–81). This is about twice the number given by Mottier. It was not till material of the reduction divisions in the megaspore mother cell was studied that the original count of thirty-six was seen (Fig. 34) by the writer. Here a few late prophases gave results approximately verifying Mottier. The megaspore metaphases were not in such a position that they could be counted. This gives a very interesting situation, since the pollen material first studied clearly represented a race with a 2x gametophytic count. As proof of two cytologically distinct lines of *Acer rubrum* this evidence is far more decisive than that for *Acer platanoides*. To add to the interest of the situation some material belonging to two other batches was found, which, though not as good as that from which the 2x gametophyte count was obtained, showed clearly that the reduced number of the chromosomes was here in the neighborhood of fifty (Figs. 82–84). If the original number of thirty-six is exactly correct, which, although it seems probable, the writer would not undertake to absolutely affirm with the few data at his disposal, then seventy-two would be the expected reduced number in the tetraploid form.

The pollen of the material above described probably represents such a race. If these hybridized, then the pollen of the hybrid form would have a count of fifty-four according to ordinary expectations, which was observed in one instance in the two fixations just mentioned, although most of the counts run from fifty to fifty-two. The seventy-two chromosome class of pollen was found in pollen of male flowers, the apparently "hybrid" condition in the pollen of both male and female flowers. Unfortunately, such a situation being totally unforseen, no records are to be had that would locate the original trees. Measurements were made to compare the size of the microspore

mother cells at the first metaphase. The longest and shortest diameters of each grain were taken and averaged for the series. The tetraploid material gave an average diameter for those counted of 29 microns, the pollen from the "hybrid" male flowers gave 23.5 microns, and the pollen from the female "hybrid" 24.8 microns. The difference between these last two is hardly significant, being probably a shrinkage variation. The volume of the tetraploid cells is therefore about 12,800 cubic microns each, and that of the larger "hybrid" material about 8,000 cubic microns, which gives a ratio somewhat less than that of the chromosome numbers, namely 4:2.5 as against 4:3.

Abnormalities in pollen formation have appeared in *Acer rubrum*, which may throw light on the origin of these conditions. In the material giving the intermediate count, one case of a tripolar spindle was found, with the chromosomes partly oriented with respect to one axis, partly with respect to the others. In different material pollen grains were found of two sizes intermixed, in diameter about 39 and 27 microns respectively. Furthermore, conditions of lack of complete separation of the original tetrad were found, both where, within the wall of the mother cell, each of the four had formed a wall of its own and also where they remained naked within the common investment. These were in anthers where the majority of the pollen grains were well advanced toward maturity. Some large grains were present with abnormal numbers of nuclei. Germination of the seeds of the Red Maple furnished material for a study of the somatic divisions, but the extreme complexity of the figures made the counting too much of a strain, and, since the accuracy was comparative at best, only a few cases were critically studied. The number of chromosomes as counted seemed to be above ninety (Figs. 76–78). Owing to the conditions mentioned it would be unwise to try to interpret this in terms of the reduced number.

Ovule Development

The only maple which has received attention with respect to the development of the ovule and embryosac is *Acer rubrum*, upon which Mottier published a paper in 1893 (12). This paper was written before some of the most important advances in methods of technic, and it was thought advantageous to follow the development again in the same species. The observations

of the writer agree for the most part with those of the earlier above-named investigator, but there are some points with regard to which the writer would like to suggest a somewhat different interpretation. To make these clear, a review of the situation will be given.

The ultimate origin of the megaspore mother cell was not determined. In material fixed about the end of October, 1918, it was already differentiated as a deeply placed cell in the forward end of the nucellus. The first ovular coat was just becoming evident at that time (Fig. 85). Little advance in the growth occurred till spring, when a rapid increase in size accompanied the growth and maturation of the stamens, and the heterotypic division in the megaspore mother cell occurred soon after the microspore cells had reached the tetrad state. Both of the ovular integuments were well developed by the time synapsis was reached (Fig. 86). This applies only to the female flowers. In the functionally male flowers the ovaries remain very small, and the carpels seem to fail to close completely, leaving a rather large opening at the stylar end. In the functionally female flowers the carpels also remain sufficiently separate at the top to leave a pore between the style bases, but this opening was filled by the abundant stylar hairs, whose walls seem to become partly gelatinized at this point.

Following the heterotypic division there is formed a wall, separating the daughter nuclei into different cells (Fig. 87). The writer was able to secure a very complete series of stages illustrating the chromatin behavior during the heterotypic division, which was fundamentally similar to the same series in the pollen formation. In connection with the discussion of the nuclear conditions in this species a megaspore prophase was used to illustrate the condition where the reduced chromosome number was thirty-six, and the same figure, showing the thirty-six paired segments nearing diakinesis, illustrates the difference in size between the microspore and megaspore mother cell nuclei (Fig. 34). So far there is no question as to the history of the megaspore.

In Mottier's paper the description of the succeeding stages is as follows: "The upper cell divides again in a similar manner, so that there are three cells resulting from the mother cell (fig. 5). The lower one of these three now enlarges gradually ab-

sorbing the two upper; its large nucleus soon divides, and the resulting nuclei move away from each other toward the opposite ends of the cell (fig. 5). The further behavior of these nuclei is similar to that which obtains in all known embryosacs of angiosperms." From his figures it seems evident that the "upper cell" means the one near the micropyle, and the "lower cell" the one near the chalaza. His description would indicate that the more micropylar cell goes through the homotypic division before there is any division in the more chalazal cell, and that following this division a wall is laid down and then the two cells thus formed degenerate. The homotypic division in the chalazal cell of the pair then follows, and both of the nuclei formed function in the maturation of the embryosac, each dividing twice to give the eight elements of the mature sac. It appeared to the writer an unusual circumstance that one cell of the original diad should go through a complete homotypic division only to degenerate, whereas in the other the nucleus only should divide and both nuclei function. In view of the more recent work in cytology it seems more to be expected that one of the cells of the original diad should degenerate without dividing, and that if the homotypic division in the other cell closed with wall formation, the daughter cell adjoining the degenerating cell should also break down. This would account for the two degenerating cells reported by Mottier, and would indicate that the nucleus in the remaining cell, morphologically equivalent to one cell of a tetrad, would have to pass through three successive free gametophytic divisions before the embryosac reached maturity, which is rather the normal history in dicotyledons. However, if Mottier actually saw the process of division of the micropylar cell of the diad, this history could not hold. But he does not figure any stage during the division, and it is easily possible to misinterpret the condition if only the final product of a row of three cells is available. The significant difference between the two possibilities lies in that in the one case only two gametophytic divisions occur, showing a tendency toward the *Lilium* type where but one is present, while in the second case the more normal number of three would be found. The question as to whether a cell which is to undergo degeneration is likely to divide earlier and in a more primitive manner (*i. e.*, with wall formation) than its sister cell which is to

function, also deserves consideration. Such material as the writer has favors the interpretation here offered, but it is not sufficiently conclusive to serve as a basis for discarding the statement of Mottier, and the question must be left open for the present.

In any event, by the time the row of three cells is formed, the ovule begins to bend downward, and the outer integument on the lower side of the ovule begins to enlarge decidedly (Fig. 88). By the time the chalazal cell of the row of three has undergone the first division the ovule has increased greatly in size, bent over nearly as far as it ever does, and it is evident that the degeneration of the two cells at the micropylar end of the row of three is far advanced. From the swelling of the outer integument the cells grow as hair-like processes (Fig. 89). The division into the four nucleate stage shows these hair cells even more elongate, and beginning to become crowded at the bottom of the ovarian cavity (Fig. 90). They subsequently form a mass of considerable size, and about the time of fertilization their walls seem to be thickened in a gelatinous manner, and evidences are present that the cavity of the ovary contains a partly coagulable liquid. The hairs may secrete a fluid which aids in the passage of the pollen tube to the micropyle.

There is rarely any evidence of the degenerating cells by the time the eight nucleate stage of the embryosac has been reached. Of these eight nuclei, three pass to the antipodal end and organize cells the membrane of which often is very indefinite. Two form synergidæ and one an egg at the micropylar end, the latter protruding into the embryosac cavity above the synergidæ. Two nuclei remain, one at each end of the sac (Fig. 36). These polar nuclei pass toward the center of the cavity, where they come into contact (Fig. 37), and then pass together to the egg, usually not fusing till they have taken up a position close above it (Figs. 38, 39). Fusion is by simple merging of the contents, no definite spireme being in evidence at this time (8). This stage is generally not reached till after the flowers have opened, and even till after pollination has taken place. The antipodal cells very soon disappear, though they may in occasional cases persist for some time (3).

Fertilization and Embryogeny

The fusion of the gametes in *Acer*, so far as observed, resembles the conditions described by Ishikawa for *Oenothera* (8). The pollen tube in entering destroys usually only one of the

synergidae, the other persisting for a short time (Fig. 40). The "filiform apparatus" was very slightly developed. As the flowering of *Acer saccharinum* upon which the writer had counted for the sequence of stages succeeding the entrance of the sperm nuclei, was followed in 1919 by a severe frost and most of the ovules rendered abnormal or infertile, a detailed discussion of the stages in fertilization will be held for another paper. As soon as the triple fusion is accomplished the endosperm nucleus passes up to the middle of the embryosac (Fig. 40). Division does not ordinarily take place till this position is reached (Fig. 42). The fertilized egg is even slower to divide, usually holding back till the eight or even the sixteen nucleate stage of the endosperm. The first wall is transverse (Fig. 41), and so is the second, but the third is vertical or oblique in the terminal cell (Fig. 43), and is followed by a similar wall in the middle cell of the original row (Fig. 44). The basal cell seems to divide once more (Figs. 45, 46), and in the later development of the embryo may divide a few times to give the irregular group of cells which form the suspensor of the embryo. The endosperm never becomes more than a sheath of protoplasm in which the free nuclei divide, at first by mitosis, and later amitotically. They become very numerous, reaching many hundreds. The cavity of the embryosac increases greatly after fertilization, and the nucellus stretches to accommodate it. This condition is especially marked in *Acer saccharinum* and *Acer platanoides*. In the latter the contents of the nucellar cells appear disintegrated, and the walls themselves later in part break down, so that by the time the embryo has reached the stage of the Red Maple embryo shown in Fig. 47, the cavity of the embryosac will have increased in volume a hundred times, and be surrounded by only a very few layers of stretched nucellar cells, except just above the micropyle, where the stretching and disintegration does not occur. The embryo occupies only a very small part of the pointed micropylar end of this cavity, and the rapid growth of the sac and disintegration of the nucellus is therefore not due to pressure from the embryo. The outer part of the second integument becomes hardened, protecting the embryo, especially in some of the exotic forms. The rapid growth of the embryo, though delayed, causes the cotyledons in many species to become crumpled in the seed. Evidence of the beginning of this con-

dition appears long before the length of the embryo equals that of the cavity, in *Acer rubrum*. The form of the embryo differs somewhat among the various species even in the early stages (Figs. 49, 50).

In most species the ovary did not grow much faster than necessary to accommodate the swelling ovules, but in others, *Acer negundo* especially, immediately after fertilization the ovarian cavity increased at a much greater rate than the ovules. The growth of the alae is initiated by pollination, progressing far before development of the embryo begins. Fertilization seems to take place about forty to seventy-two hours after pollination.

Abnormalities in embryosac development were many. It is to be remembered that of the two ovules formed in each cavity of the ovary only one comes to maturity, and that even in the flowers that are developing normally half the embryosacs seen will be in stages of abnormal development or degeneration. The presence of sterile flowers increases the number of atypical cases. The frost mentioned above seemed to destroy the egg first, so that a several-nucleate endosperm with a shriveling egg, as well as other degenerate conditions, was found in material gathered on the days succeeding the cold spell.

In one ovule of *Acer platanoides* an embryosac with a double embryo appeared. The second appeared as a smaller individual, attached to the base of the primary one. It possibly resulted from a bifurcation of the head end of the embryo while small, after which one of the halves greatly out-grew the other (Figs. 91, 92).

Seedling Anatomy

A study of the anatomy of the developing Maple seedling offers little of itself, but a comparison of the normal with a tricotyledonous specimen which sprouted in one of the cultures is of interest. The development in maples of specimens with abnormal numbers of cotyledons and of later leaves in whorls of three or even more is well known (15) as is also twinning, etc. (5).

In *Acer rubrum* the cotyledons have in the contracted lower part of the blade about six vascular strands (Fig. 93). These unite in the petiolar part to two (Figs. 94, 95) which pass unfused into the hypocotyl (Figs. 95, 96). The plumule at first

shows only one strand in each leaf, but as they grow three become evident which fuse in the petioles or, lower, in the hypocotyl (Figs. 94, 95). The bundles which supply the plumule become less and less prominent as one descends the axis, the xylem disappearing and the phloem fusing laterally with the adjacent bundles supplying the cotyledons (Figs. 96, 97), till at last there is a simple axis with four collateral bundles (Fig. 98). These form the four poles of the tetrarch root by simple rotation of the elements (Figs. 99, 100, 101).

In the same species the tricotyledonous specimen was prepared in serial sections, and the vascular strands traced in the same way. In the upper part of the cotyledons there were about the same number of vascular strands as in the cotyledons of the normal form. Toward the petiolar base in two of them the strands partially united (Figs. 102, 103), to reappear again in the hypocotyl as two distinct but closely placed bundles (Fig. 104). The third cotyledon possessed a small lobe near the base (Fig. 102) which united with it before union with the axis occurred. In this case the two bundles at the base remained widely separated, a small patch of phloem tissue remaining between them (Figs. 103, 104). There were three plumular leaves, all prominently three-lobed. These had each three vascular strands, which remained distinct into the hypocotyl, where the xylem of the lateral members of each group disappeared, and the phloem of these fused with the central member (Figs. 102, 103, 104). Instead of becoming united into four bundles in the upper hypocotyl as in the normal specimens, the bundles from cotyledons and plumule formed an irregular ring (Fig. 105). A bend above the base of the hypocotyl made it impossible to determine whether these fused to a regular number in the lower hypocotyl, or, as seems likely from the irregular distribution of the xylem (Fig. 106), merged in the transition zone at the base of the hypocotyl. There the vascular system appeared as an irregular ring, the xylem elements on the inner margin. In the top of the root these passed out toward the periphery at four points (Fig. 107) forming a tetrarch root that was somewhat more irregular in form than the normal (Fig. 108).

The condition indicated seems to be that of a simple fission of one of the two typical cotyledons carried to its greatest extent, the bundles supplying each part being distinct far down the

hypocotyl. The small lobe at the base of the third cotyledon may or may not represent a partial development of the same kind.

Summary

The Maples studied, with one exception, *Acer saccharinum*, mature their pollen during the expansion of the buds in the spring. *Acer saccharinum* matures its grains to the one nucleate stage in the autumn, the division to form the tube and generative nuclei generally being delayed till shortly before flowering. It is the first of the genus to bloom, being followed at intervals by the other native forms, the exotic species closing the series about the end of April.

Pollen development in *Acer negundo* proceeds much as described by Mottier, and in the other Maples studied the process is similar. The haploid chromosome number is thirteen. Haploid counts were made in *Acer platanoides* showing eleven, in *Acer saccharum* showing thirteen, in *Acer pseudo-platanus* showing twenty-six, in *Acer saccharinum* showing twenty-six, and in *Acer rubrum* showing approximately seventy-two, fifty-four and (megaspore mother cell) thirty-six chromosomes.

Somatic counts were made in the root-tips of some species with the following results: *Acer platanoides*, twenty-six; *Acer pseudo-platanus*, fifty-two; *Acer saccharinum*, fifty-two, with also isolated cells containing about twice that number; *Acer carpinifolium*, fifty-two; and *Acer rubrum*, above ninety. The difference between the somatic and reduced counts in *Acer platanoides* may be due to differing strains with differing nuclear composition. The conditions in *Acer rubrum* seem to indicate that a tetraploid form exists, and the intermediate counts similarly seem to indicate that hybrids with the normal diploid form occur.

Ovule development was followed in *Acer rubrum* and other species, with in the species named a row of three potential megaspores resulting from the divisions of the mother cell. The chalazal one persists, the other two degenerate. The persistent cell gives rise to the embryosac, which is normal with eight nuclei. The polar nuclei fuse before fertilization and the endosperm nucleus passes to the middle of the sac before dividing. The embryosac enlarges greatly, especially in *Acer platanoides*, and many free endosperm nuclei are produced, but no cell walls are laid down. The growth of the embryo does not accompany

that of the ovular cavity, but is at first delayed, later progressing more rapidly so as to fill the cavity often with accompanying crumpling of the cotyledons.

Abnormalities of pollen formation, such as giant grains and unseparated tetrads, were seen, and also abnormalities in the formation of the embryosac. Tricarpellary ovaries appeared in several forms, and a twin embryo was observed, with one individual much larger than the other.

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Explanation of Plates

Plate VI—Stages in Reduction Divisions, Pollen Formation in *Acer negundo*. All Figures Reproduced ×2250.

Fig. 1. Resting nucleus after last archesporial division.

Fig. 2. Nucleus showing approaching leptonema.

Fig. 3. Leptonema entering synapsis as a network.
Fig. 4. Mid-synapsis.
Fig. 5. Looped pachynema threads leaving synapsis.
Fig. 6. Ditto.
Fig. 7. Hollow spireme.
Fig. 8. Contracting hollow spireme passing into strepsinema.
Fig. 9. Early strepsinema.
Fig. 10. Strepsinema, thread breaking up.
Fig. 11. Strepsinema, thread largely broken into chromosome segments.
Fig. 12. Ring-like chromosome segments.
Fig. 13. Ditto.
Fig. 14. Breakdown of the nuclear membrane, strands of cytoplasm traversing the cavity.
Fig. 15. Polar view, heterotypic metaphase, showing thirteen chromosomes, haploid number.
Fig. 16. Side View, heterotypic anaphase.

PLATE VII—Stages in Reduction Divisions, Pollen Formation in *Acer negundo* (Figs. 17–26), *Acer rubrum* (Figs. 28–30), and Pollen Grain of *Acer saccharinum* (Fig. 27). All except Fig. 27 reproduced ×2250.
Fig. 17. Multipolar spindle, early with large nucleolus.
Fig. 18. Multipolar spindle, later, with smaller nucleolus (in center).
Fig. 19. Side view, telophase of heterotypic division.
Fig. 20. Polar view, telophase of heterotypic division, showing thirteen chromosomes.
Fig. 21. Late telophase, showing formation of nucleolus, the large body in center of nucleus.
Fig. 22. Nucleus during interkinesis.
Fig. 23. Prophase of homotypic division.
Fig. 24. Polar view, breakdown of nuclearmembrane, homotypic division, nucleolus evident.
Fig. 25. Multipolar spindle, homotypic division, showing the remains of the homotypic spindle, and the nucleoli near the periphery of the cell.
Fig. 26. Homotypic division, side and polar views, showing remains of heterotypic spindle and thirteen chromosomes in the polar view of the metaphase.
Fig. 27. Pollen grain, mature state, with tube and generative nuclei, *Acer saccharinum*. ×950.
Fig. 28. Strepsinema, *Acer rubrum*.
Fig. 29. Side view, heterotypic metaphase, showing chromosome pairs and polar position of the dense mass of cytoplasm. Seventy-two chromosome form.
Fig. 30. Polar view, heterotypic metaphase, showing lateral position of the dense cytoplasmic mass. Shows count of seventy-two chromosomes.

PLATE VIII—Tapetal Cells of *Acer negundo* (Figs. 31–33), Embryosac and Embryo Formation in *Acer rubrum* (Figs. 34–41, 43–49), Embryosac and Embryo of *Acer saccharinum* (Figs. 42, 50). Reproduced ×200, except as indicated.

Fig. 31. Tapetum cells, showing amitotic nuclear division. ×900.
Fig. 32. Ditto. ×900.
Fig. 33. Tapetum cells, showing mitotic nuclear division. ×900.
Fig. 34. Megaspore mother cell, early diakinesis, showing about thirty-six chromosome pairs. ×2250.
Fig. 35. Row of three megaspores, micropylar pair degenerating, chalazal undergoing nuclear division.
Fig. 36. Embryosac before migration of the polar nuclei to the center of the embryosac.
Fig. 37. Meeting of the polar nuclei at the center.
Fig. 38. Fusion of the polar nuclei after reaching the egg. The nuclear membranes between the nuclei have disappeared. ×470.
Fig. 39. Mature embryosac ready for fertilization.
Fig. 40. Embryosac shortly after fertilization. One of the synergidæ has been destroyed, the other is disintegrating but the nucleus is evident. The dark mass introduced by the pollen tube is present, and the endosperm nucleus has begun to move toward the center of the embryosac.
Fig. 41. Two cell stage of the embryo, eight nucleate endosperm.
Fig. 42. Fertilized embryosac before division of endosperm nucleus.
Fig. 43. Four-celled embryo.
Fig. 44. Five-celled embryo.
Fig. 45. Nine-celled embryo.
Fig. 46. Eight (?) celled embryo.
Fig. 47. Older embryo.
Fig. 48. Embryo showing beginning of the two cotyledons. ×25.
Fig. 49. Older embryo of *Acer rubrum*. ×25.
Fig. 50. Older embryo of *Acer saccharinum*. ×25.

Plate IX—Chromosome Counts in Various Maples. All figures reproduced ×2250.

Fig. 51. Upper and lower groups, heterotypic anaphase in *Acer negundo*. Thirteen chromosomes in each case.
Fig. 52. Metaphase plate, homotypic division, *Acer negundo*, showing thirteen chromosomes.
Fig. 53. Ditto, another case.
Fig. 54. Metaphase plate, heterotypic division, *Acer negundo*, showing thirteen chromosomes.
Fig. 55. Ditto, another case.
Fig. 56. Ditto, another case.
Fig. 57. Metaphase plate, division in root-tip, *Acer platanoides*, showing twenty-six chromosomes.
Fig. 58. Ditto, another case.
Fig. 59. Metaphase plate, heterotypic division, *Acer platanoides*, showing eleven chromosomes.
Fig. 60. Ditto, another case.
Fig. 61. Anaphase group, heterotypic mitosis, *Acer platanoides*, showing eleven chromosomes.
Fig. 62. Ditto, the other group from the same cell.

Fig. 63. Metaphase plate, division in root-tip cell, *Acer pseudoplatanus*, showing fifty-two chromosomes.
Fig. 64. Ditto, another case.
Fig. 65. Metaphase plate, heterotypic division, *Acer pseudo-platanus*, showing twenty-six chromosomes.
Fig. 66. Ditto, another case.
Fig. 67. Metaphase plate, division in root-tip cell, *Acer carpinifolium*, showing apparently fifty-five chromosomes.
Fig. 68. Ditto, another case, with the more frequently found number of fifty-two chromosomes.
Fig. 69. Metaphase plate, heterotypic division, *Acer saccharum*, showing thirteen chromosomes.
Fig. 70. Anaphase plate, heterotypic division, *Acer saccharum*, showing twelve chromosomes.
Fig. 71. Ditto, other plate in small cell, showing thirteen chromosomes.
Fig. 72. Metaphase plate, division in root-tip cell, *Acer saccharinum*, showing fifty-two chromosomes.
Fig. 73. Anaphase groups, division in pollen grain to form tube and generative nuclei, *Acer saccharinum*, showing twenty-six and (?) twenty-seven chromosomes.
Fig. 74. Metaphase plate, division in root-tip cell, *Acer saccharinum*, showing ninety-one (or more) chromosomes, approaching twice the normal number.
Fig. 75. Ditto, ordinary cell, showing fifty-two chromosomes.
Fig. 76. Metaphase plate, division in root-tip cell, *Acer rubrum*, showing ninety (or more) chromosomes.
Fig. 77. Ditto, showing eighty-eight (or more) chromosomes.
Fig. 78. Ditto, showing ninety-four (or more) chromosomes.

PLATE X—Chromosome Counts and Ovule Development in *Acer rubrum*, Abnormal Embryo in *Acer platanoides* (Figs. 79–84 ×2250, Figs. 85–90 ×135).

Fig. 79. Metaphase plate, heterotypic division, showing seventy chromosomes.
Fig. 80. Ditto, showing sixty-eight chromosomes.
Fig. 81. Ditto, showing sixty-seven chromosomes.
Fig. 82. Ditto, showing fifty-three chromosomes.
Fig. 83. Ditto, showing fifty-four chromosomes.
Fig. 84. Anaphase groups, heterotypic division, showing fifty-two and forty-eight chromosomes.
Fig. 85. Ovule, resting condition in late autumn.
Fig. 86. Ditto, at time of synapsis.
Fig. 87. Ditto, after heterotypic division, showing two cells derived from megaspore mother cell.
Fig. 88. Ditto, showing row of three potential megaspores.
Fig. 89. Ditto, showing micropylar two in row degenerating, chalazal cell in the two nucleate stage of the embryo-sac.
Fig. 90. Ditto, embryosac cell in four nucleate stage.

Fig. 91. Twin Embryo, *Acer platanoides*, showing cells of the smaller embryo. ×200.

Fig. 92. Ditto, showing attachment region of the embryos. ×200.

PLATE XI—Dicotyledonous and Tricotyledonous Seedling Structure in *Acer rubrum*. All Figures ×30.

Fig. 93. Dicotyledonous seedling section through lower part of blade of cotyledons.

Fig. 94. Ditto, section through upper part of cotyledonary petioles.

Fig. 95. Ditto, through junction of cotyledons with hypocotyl.

Fig. 96. Ditto, just below cotyledonary node.

Fig. 97. Ditto, a little lower than Fig. 96.

Fig. 98. Ditto, through middle region of hypocotyl.

Fig. 99. Ditto, at top of transition region near base of the hypocotyl, showing bundle ring.

Fig. 100. Ditto, lower, showing passage of xylem toward the periphery at four points, in the top of the root.

Fig. 101. Ditto, lower, in main root axis, showing tetrarch character.

Fig. 102. Tricotyledonous embryo, section through lower part of blade of cotyledons.

Fig. 103. Ditto, through junction of cotyledons with hypocotyl.

Fig. 104. Ditto, just below cotyledonary node.

Fig. 105. Ditto, through middle region of hypocotyl.

Fig. 106. Ditto, through top of transition region near base of the hypocotyl, showing bundle ring.

Fig. 107. Ditto, lower, showing passage of xylem toward the periphery at four points, in the top of the root.

Fig. 108. Ditto, lower, in main root axis, showing irregular tetrarch structure.

NOTE—All drawings of cytological details except stages in the development of the embryosac were drawn at a magnification of 3,380 diameters. Other details were drawn at lesser magnifications, and all figures except those on Plate XI have been reduced in reproduction to two-thirds of the original size. The figures of seedling structure were drawn at 75 diameters and reduced to 30 diameters in reproduction.

THE MORPHOLOGICAL CONTINUITY OF SCROPHULARIACEAE AND OROBANCHACEAE

BY

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With Plates XII–XVI.

(Thesis presented to the Faculty of the Graduate School in partial fulfilment of the Requirements for the Degree of Doctor of Philosophy.)

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Introduction

In the past, the genera of Orobanchaceae have been regarded as of nearest affinities with the Gesneraceae; this wholly because of the one-celled ovary. But such a proceeding only takes account of one morphological detail. Is there any other family with which Orobanchaceae can be directly and continuously connected in many morphological features? The group, being wholly parasitic, must of necessity be derived as an offshoot from some family wholly free or more or less parasitic in habit.

The only related family showing such is Scrophulariaceae. While the majority of these in genera are green and independent in their nutrition, others show all stages in degradation-transitions to reduced green root parasites, thence to yellowish, or red-yellow parasites, finally to degraded simplified parasites that are wholly heterotrophic (*Harveya*, *Hyobanche*). Thus, for example, in the single genus *Gerardia* of the Eastern United States some species are tall leafy plants, as in *G. flava*, and these show slight root parasitism. Transitions can be traced from this to *G. pedicularia*, thence to *G. purpurea*, to *G. oligophylla*, and to *G. aphylla*, the last of which has scant twigs and small leaves that may be almost absorbed. The flowers in the latter are few and reduced in size, while parasitism is almost completely established in relation to other plants. From such forms transition is easy and gradual to *Striga*, *Harveya*, and *Hyobanche*. But between *Harveya* and *G. aphylla* on the one hand, or species of *Orobanche* on the other, the macroscopic and microscopic resemblances, as will afterward be shown in this paper, are graded and complete. Is then the fundamental resemblance to Gesneraceae of a one-celled ovary as compared with Scrophulariaceae with its two-celled ovary fundamental and indicative of true affinity? This question will be fully worked out in a later part of the paper. But attention might now be drawn to some comparative morphological facts that may shed light on the present problem.

If we review the more pronounced saprophytic families of flowering plants, like Burmanniaceae, Orchidaceae, Ericaceae, (including Monotropaceae) and Gentianaceae, all show degra-

dation-transitions from green strongly vegetative plants of independent nutrition, to others with feeble root saprophytism and thence to highly degraded colorless and heterotrophic plants like *Thismia* of Burmanniaceae, colorless genera like *Epipogon*, *Aphyllorchis*, *Neottia*, and *Corallorhiza* in Orchidaceae, colorless *Monotropa* and other genera of the Ericaceae, and the colorless *Leiphaimos* in Gentianaceae. Now in all of these, distinct and continuous transition is seen from five-celled, three-celled, or two-celled states (Ericaceae, Burmanniaceae, Orchidaceae, two-celled Gentianaceae) of the ovary to incompletely five-three or two-celled, and ultimately a one-celled state with parietal placentation. Such might, therefore, suggest that Orobanchaceae simply represents a greatly degraded offshoot series or sub-family of parasitic habit that has gradually been derived from Scrophulariaceae in which slow absorption of the ovarian partitions has resulted in a one-celled state from a primitively two-celled. If such be true, then varied morphological transsitional characters should be traceable between Scrophulariaceae and Orobanchaceae, while correlated with this a graded physiological parasitism and degradation should also be observed. It is the aim of the present thesis to demonstrate that such is correct.

In undertaking this, the writer might first review the varied opinions held by previous observers.

Review of Literature and Discussion

Wettstein (1, p. 48) separates the Scrophulariaceae from the Orobanchaceae and Gesneraceae on account of the one-celled ovary in the last two. He states that a great many Scrophulariaceae have close affinities with other families. "Die Orobanchaceae und Gesneriaceae lassen sich durch den 1 fächerigen Frkn. mit parietaler Placentation . . . . von den Scrophulariaceae unterscheiden." He then states that clear connections are shown in the genera *Harveya*, *Hyobanche*, and *Buchnera* of Scrophulariaceae with Orobanchaceae.

Beck (2, p. 128) makes this statement: "The Orobanchaceae, which are frequently regarded as a parasitic side line of the Gesneraceae, are separated from the Gesneraceae through the perfect superior fruit, from the Cyrtandreae through the richly de-

veloped endosperm and the undeveloped endosperm of the seed . . . . from both especially through their parasitism. The one-celled fruit separates them from the Scrophulariaceae with which they have also much in common." (Present Author's Trans.)

Fritsch (3, p. 141) under the Gesneraceae treats the connections of Gesneraceae with related families, especially with the Scrophulariaceae, Orobanchaceae and Bignoniaceae, and holds that a sharp distinction can scarcely be drawn between these families. He further says, "Hingegen stehen die Orobanchaceae den Gesneraceae so nahe, dass die Auffassung derselben als einer parasitischen, laubblattlosen Unterabteilung der Gesneriaceae keinen grossen Fehler involvieren dürfte. Immerhin ist die Placentation und der Bau des Frkn. überhaupt ein Unterscheidungsmal zwischen den Gesneriaceae, Orobanchaceae und Scrophulariaceae."

Baillon (4) makes no comparison of the Scrophulariaceae with the Gesneraceae and Orobanchaceae. He does not consider the Gesneraceae and Orobanchaceae as two separate families, but regards the Orobanchaceae (of other authors) as a parasitic series of the Gesneraceae.

LeMaout and Decaisne (5, p. 593) include the genus *Hyobanche* in the Orobanchaceae, though on account of its two-celled ovary, most authors place it in the Scrophulariaceae. The following is stated: "Orobanchaceae approach the Scrophulariaceae in their regular corolla, didynamous stamens, capsular fruit, and albuminous embryo; they differ in their leafless and scaly stem and parietal placentation. This placentation, their glandular disk, and the preceding characters ally them to Gesneraceae, from which they are separated by their scattered scales, parasitism, hypogynous corolla, and basilar embryo."

Warming (6, p. 525–28) places *Lathraea* in the family of Scrophulariaceae. The plant is described as pale yellow, or reddish (without chlorophyll); it is parasitic on the roots of the Hazel, Beech, and other shrubs or trees, having an aerial stem, and an underground perennial rhizome ,covered with opposite, scale-like, more or less fleshy leaves. It approaches Gesneraceae in having a unilocular ovary with two parietal placentae. With him Orobanchaceae finds no place as a family, the genus *Orobanche* being included in the Gesneraceae. "Orobanche (Broomrape) is allied to this order as a parasitic form."

Perhaps the most extensive morphological and physiological studies of parasitic Scrophulariaceae and Orobanchaceae have been made by Heinricher (7, p. 390-451, 665-773) and Solms-Laubach (8, p. 560-75) on the former, by Beck (9, p. 7-70) and Koch (10,) on the latter. The work on such genera as *Euphrasia*, *Odontites*, *Pedicularis* and not least *Bartsia* and *Tozzia*, by Heinricher has a very definite bearing on the present investigation. To quote from him on *Bartsia* and *Tozzia*: "In der That sind es diese beiden Rhinanthaceen, welche uns die Brücke von den halbparasitischen Rhinanthaceen zu der holoparasitischen Gattung *Lathraea* bauen. . . . Der Aufbau des Lathraea- Rhizoms ähnelt sehr dem von *Bartsia*, die Unterschiede sind wesentlich dadurch bedingt, das erstere Holo-, letztere Hemiparasit ist. . . . . *Tozzia* nimmt eine ganz eigene Stellung in der Rhinanthaceen-Rheihe ein; sie ist nicht Holoparasit und nicht Hemiparasit, sondern sie ist beides in zeitlicher Folge. Und so wird sie eben zum biologischen Bindeglied Zwischen den Halbschmarotzern und der Holoparasitischen Gattung *Lathraea*."

In view of the above comparative estimates of different authors, the question at issue resolves itself into one of three positions. (1) The Gesneraceae and Orobanchaceae are most nearly related to each other in that they both possess a one-celled ovary with deep to shallow parietal placentation. (2) Orobanchaceae and Scrophulariaceae are most nearly related to each other in their root parasitism, their alternate or at times opposite leaves, their progressive parasitic degradation, condensation of axis, and eventually non-chlorophylloid aspect. They only differ in the two-celled ovary, but Scrophulariaceae seem to be united with Orobanchaceae by *Christisonia neilgherrica*, with its two-celled, becoming above one-celled ovary, as well as by *Lathraea* with its imperfectly two-celled ovary. (3) The Orobanchaceae stand by themselves as a family.

To take the last caption first, Orobanchaceae being wholly parasitic and non-chlorophylloid, clearly suggests that physiologically and now morphologically it is a degenerate offshoot from some family that tended gradually to show semi-parasitic habit. Now of all the Bilabiatae, there is only one other family which shows, like Orobanchaceae, parasitic habits, namely, Scrophulariaceae. No Gesneraceae are parasitic, or even show a slight

beginning of parasitism. Such being the case, the second becomes that which we are inclined to favor. But the two-celled ovary of Scrophulariaceae and the one-celled ovary of the Orobanchaceae has been the barrier to such a connection with morphologists in the past.

As a preliminary, therefore, to subsequent studies and investigation it may be profitable to compare groups of parasitic and saprophytic plants already known to us. To start with saprophytic families first, it is well known as already shortly stated above, that in the Burmanniaceae the green and least degraded genera, such as *Burmannia*, have three-celled ovary with central placentation, while in *Gymnosiphon* and the most degraded genera like *Thismia* and *Arachnites* the ovary has become one-celled with deep to shallow parietal placentas.

In the large family of the Orchidaceae as now recognized by systematists the most primitive subdivision Apostasieae, has subregular flowers, three to two stamens, and a three-celled ovary to the pistil. In the more evolved subdivision Selenipedieae, the flowers are decidedly irregular, the stamens are two in number, and the ovary is three-celled. Root saprophytism in its commencing stages is amongst these not uncommon. In the division Cypripedieae, the stamens are still two in number, but the ovary usually has become one-celled by varying stages of reduction in ingrowth of the carpellary margins by graded steps that can well be traced. Saprophytism is a frequent feature of their roots. In the division Orchideae, the flowers are most varied and highly specialized, the stamens are now reduced to one functional, the ovary is one-celled with shallow parietal placentas. In this division all stages of condensing degradation and loss of chlorophyll can be observed, till such non-chlorophylloid and greatly degraded genera like *Neottia* and *Corallorhiza* are reached. Unquestionably here a continuous process of condensing reduction and degradation in the above more or less related genera is correlated with increasing saprophytism, all of this being associated with a gradual transition from three-celled ovary to one-celled ovary with deep placentas and thence to one-celled ovary with shallow marginal placentas.

Again, the family Ericaceae when treated in the only appropriate morphological manner that explains the evolution of the subdivisions satisfactorily, includes primitive shrubby plants

with ample green leaves that have evolved along at least three main lines. One line, as beautifully traced by Dr. Henderson (11) in a recent paper, shows condensing and degrading simplification through saprophytism till low herbaceous shrubs with few scattered leaves like *Chimaphila* are reached, while these lead to the colorless greatly degraded genera of the Monotropaceae like *Sarcodes* and *Monotropa*. Still another line leads to the parasitic Lennoaceae, the carpels of which have probably increased in number by subdivision of a primitive five, that remain as many celled but the ovules have become reduced to two or one in each cavity. A third line passes to highly evolved types like the Azaleas, Kalmias, and Rhododendrons with ample leafage, and roots that are nonsaprophytic or only slightly saprophytic and ovary that is five-celled.

In the Gentianaceae, that frequently tend to be slightly or markedly saprophytic, the ovary is still two-celled in the subdivision Exacineae. In others like Lisiantheae the ovary is strictly one-celled but has deep almost adjacent placental ridges. In the Gentianeae the one-celled ovary has shallow ridges that reach a climax of shallowness in the colorless degraded saprophytes *Voyria* and *Leiphaimos*.

In the Convolvulaceae the ovary throughout is typically two-celled and this is retained in species generally of the parasitic genus *Cuscuta*, but a one-celled parietal condition is present in *Erycibe*. Similarly in Rafflesiaceae, the ovary is one-celled.

From the above it is abundantly evident that alike in saprophytic and parasitic families simplifying and degrading saprophytism and parasitism nearly always are accompanied by a transition from a several-celled central type of placentation to a one-celled parietal type.

Accepting the foregoing as an indubitable fact, the question may now be asked: Can close morphological affinity be traced from Scrophulariaceae through types that become more or less parasitic and eventually degraded colorless parasites, to forms typical of the purely parasitic and non-chlorophylloid Orobanchaceae? The demonstration of this is the main thesis of the present paper. As strongly favoring such a position, it may be noted that in such a genus as *Gerardia* the most gradual transition can be traced from tall leafy green species, like *G. flava* (*Aureolaria villosa*) to *G. pedicularia*, thence to *G. purpurea*, to *G. oli-*

gophylla with few pale green leaves and branches that mainly carry on food elaboration, and finally to the most degraded member, *G. aphylla*, in which the leaves are small pale green scales, still, however, provided with a few stomata, but which are in the last stages of disappearance. It is of interest to note the close resemblance in habit, structure, etc., between the two latter types and such South African genera as *Striga* and *Harveya*, which connect again with *Hyobanche*. All of these, but the last in particular, closely simulate members of the so-called Orobanchaceae. Further, it is important to note that in the genus *Christisonia* (*Campbellia*), the ovary, while mainly one-celled with deep placental ledges, is in most of the nine species of *Christisonia* two-celled in the lower part. And so Beck (12, p. 131) has well noted, "Ausnahmsweise kammt bei letzterer ein unteren Teile 2 fächeriger Frkn. vor; es besteht somit eine starke Annäherung an die Gatt. *Harveya*." Regarding *Christisonia neilgherrica* Worsdell (13, p. 131) says, "The ovary is bilocular in its lower region and unilocular above; in the latter case the placentation is parietal. In this plant the basal portions of the two bipartite placentas very nearly meet in the centre. In the lower, bilocular part of the ovary, where the projections have become united to form a dividing wall, the placentation is axile, two placentas, bearing a large number of minute ovules, projecting into each cavity."

If the above morphological and physiological lines of continuity express a correct interpretation of the lines of evolution pursued, it should be possible to trace certain fairly continuous morphological similarities as well as degradation-differences, proceeding in relation to the following parts.

First, since the phenomenon is fundamentally due to increasing root parasitism, we should expect to find that the root and gradually thereafter the vegetative stem system should show condensation and swelling of the condensing axis, or, that this axis should become rather starved and simplified.

Second, in such condensed axes an increasing preponderance in relative width and importance of phloem over xylem should occur until in the most condensed genera it would become a preponderant feature.

Third, in the above process and with the increasing parasitic degradation the leaves would tend by degrees to become reduc-

ed in size, and in nutritive capacity, till they would become reduced to relatively small colorless scales.

Fourth, according as parasitic connection might become accentuated with herbaceous plants on one hand or with arborescent plants on the other, in corresponding degree might at least two lines of evolution open up; one in which entire plants parasitic on short-lived herbaceous hosts would become soft and degraded, while on the other hand, genera parasitic on roots of woody and not least arborescent types, might become in corresponding measure perennial and enlarged in the infesting region.

Detailed comparison will now be made.

General Morphology of the Root

In commencing parasitism as shown and illustrated in *G. flava* (Plate XII, Fig. 1) the matured perennial primary root system is spreading, loose, and expanded, covering a large area. From this expanded primary root system, secondary rootlets pass outward and downward and some of these end in parasitic suckers. The roots are firm, strong, fibrous, and play no small part in collecting raw material from the soil. The plant still depends largely upon crude sap obtained directly from the soil for its sustenance, and could possibly live an independent existence as Kerner (14, p. 180) has stated for *Odontites*.

In *G. pedicularia* the root system is more condensed and suckers are more abundant.

In *G. purpurea* (Plate XII, Fig. 2) the secondary root system, though delicate, is more condensed with numerous sucker enlargements on a variety of plants such as Grasses, Composites, etc. The main root from which these side rootlets arise is condensed and shortened.

From the short condensed primary root of *G. aphylla* (Plate XII, Fig. 3) spring the secondary roots which are less spreading than in the previous two species, wholly indicating a more closely dependent parasitism on host roots. These are smaller than the roots previously mentioned, being thin and fibrous with abundant suckers.

Drawings of the above were made to illustrate natural size as nearly as possible and to show the extent of primary and secondary roots.

In the transition from the above types the Scrophulariaceae are connected with the Orobanchaceae by the genera *Lathraea*,

and *Christisonia*. The extent of the root system of *Lathraea* is very limited; the roots are semi-woody semi-fibrous. This genus, as already pointed out, is by some authors regarded as a member of the Scrophulariaceae, by others as a member of the Orobanchaceae. It offers a graded transition from pale green and greenish purple to purple red genera like *Buchnera, Harveya* and *Hyobanche* of the Scrophulariaceae to *Orobanche* of the Orobanchaceae. Kerner (15, p. 182) has described the parasitism of *Lathraea*. He says: "The young root of the seedling grows at first at the expense of reserve material stored in the seed, penetrates vertically into the earth and sends out lateral branches, which, like the main root, follow a serpentine course and search in the loose damp earth for a suitable nutrient substratum. If one of these meets with a living root belonging to an ash, poplar, hornbeam, hazel, or other angiospermous tree, it fastens on to it at once and develops suckers at the points of contact; these suckers are at first shaped like spherical buttons, but soon acquire, as their size increases, the form of discs adherent to the host's root by the flattened side and with the convex hemispherical side turned toward the rootlet of the parasite. These discoid suckers cling to the root attacked by means of a viscid substance produced by the outermost layer of cells. As in the case of the parasites already described, a bundle of absorption-cells grows out of the core of each sucker into the root of the plant serving as the host, and the tips of the absorbent cells reach to the wood of the root" . . . . . "The roots, which issued originally from the seedling, and their suckers have long since ceased to meet the requirements in respect to nourishment of so greatly augmented a structure, and therefore additional adventitious roots are produced every year, springing from the stem and growing towards living woody branches of the thickness of a finger, belonging to the root of the tree or shrub that serves as host. When there, they bifurcate, forming numerous thickish filiform arms, which lay themselves upon the bark of the nutrient root and weave a regular web over it. Sometimes two or three of these root filaments of the parasite coalesce, forming tendrils, and the resemblance to a lace-work or braid is then all the more pronounced. Suckers, such as have been described, are developed by these root-filaments laterally, and more especially on the ends of the branches."

Did we know the parasitic root relations of *Harveya* and *Hyobanche*, these in all probability form a more perfectly graded connection between the two supposed distinct orders.

From the above we pass to *Orobanche*, e. g., *O. minor* (Plate XII, Fig. 4), in which a dense mass of secondary roots starts from a swollen shortened primary-root and these roots form by their surfaces intimate and close connections with the host roots, as described and figured by Koch (16). In *O. cruenta* the primary root swelling becomes more pronounced and the place of junction between stem and root is collar-like in appearance. Here two lines of deviation seem to start in condensing degradation.

One line, simplifying and short-lived, leads to *Aphyllon* (Plate XIII, Fig. 6) in which as figured by the writer there is even more close and extensive parasitic connection with the host than in the previous types and the parasite itself, in that secondary and probably primary roots parasitize. At the base of the short stem arises the primary root, now slightly swollen, and from this are given off secondary roots in such numbers as to form a very much tangled mass.

Another line leads to the larger stronger genus *Epiphegus* (Plate XIII, Fig. 7) of annual duration, in which a tuberous swelling from a half inch to an inch across represents a fused primary root below and a greatly condensed vegetative stem-axis above. From the lower part or primary root short and now functionless rootlets start, while from the condensed stem adventitious roots, similar in relation to the secondary ones, arise at any point of the stem axis. Accordingly parasitic connection with the host is easily and directly made by the germinating primary root as already pointed out by Cooke and Schively (17). The roots of *Epiphegus* form around and above the beech roots on which this is parasitic. The secondary and adventitious roots are short and delicate.

In *Conopholis* (Plate XVI, Fig. 33), which may be regarded as the climax type of the group, the root system so far as known is entirely hidden from external view, being represented by a large swelling and which usually terminates the oak root on which it grows. Alike roots and leaves have been entirely absorbed, although in *Epiphegus* rudiments of both are present. From the swelling arise numerous flowering shoots.

Further comparison of the last three genera will show that the parasitic roots of *Aphyllon* do not cause truncation and decay of the host roots, the latter remaining alive beyond the point of attack, while in *Epiphegus* and *Conopholis* so complete is the parasitism that host roots rarely remain alive beyond the point of parasitic attachment. In almost all of the genera of the Orobanchaceae parasitism has become highly specialized with regard to selection of hosts.

Thus a continuous and easy gradation is traced from green and nearly independent Scrophulariaceae to highly condensed and degraded Orobanchaceae, which in *Conopholis* closely simulates the most degraded representatives of the Balanophoraceae and Rafflesiaceae. On the other hand, no even approximate or suggested such connection is shown between Gesneraceae and Orobanchaceae.

Histology of the Root

In all the species of *Gerardia* examined the internal structure of the roots is of the radial polyarch type. The xylem is greatly in excess of the phloem and consists in young roots, like those of *G. purpurea*, mainly of large pitted vessels; spiral tracheae and xylem cells make up the rest of the xylem. The phloem arms alternate with the xylem and are composed of the usual elements. In older roots of *G. purpurea*, *G. flava*, *G. aphylla*, the bundle system assumes a woody more dense character, having the appearance of a ring of wood not unlike that seen in a dicotyledonous stem, save for the presence of the phloem. A considerable amount of hard bast develops. A several-layered pericambium surrounds the bundle region and this in turn is surrounded by an endodermal layer, easily recognized in young roots. The cortex is variously developed: in small, young roots it consists of cells in rows, of 2 to 3 cells in each, and these are radially disposed and connect the epidermis with the other tissues, while between these radial arms are very large open spaces; in older roots the cortical space is filled with normal thin-walled cells; in more mature roots of *G. flava* the cortex is composed almost wholly of scleroid cells staining a deep red color in safranin. In mature roots the epidermis may be replaced by cork tissue. Root hairs were also noted.

In the parasitism of *Gerardia* the roots produce swellings in the regions of contact with the host, which become hemispher-

ical and grow down the sides of the host roots but do not completely surround them. Sections of swellings show an epidermis, a cortex, and bundle elements. The most conspicuous feature of the bundles is the large number of cells with pitted walls. The cells in the upper part of the swelling have not fused to any great extent to form vessels, but in the lower spread-out part of the swelling they have the appearance of vessels (with pitted-reticulate thickenings in their walls) which establish a connection with the xylem of the host roots. This was seen in *purpurea* and *pedicularia*.

Roots of *Harveya* and *Hyobanche* were not available for investigation.

Transverse sections of the roots of *Lathraea japonica* show the epidermis, a narrow cortex, and the polyarch bundle system. In the latter unusually large pitted vessels make up the greater part of the bundles.

The roots of *Aphyllon* are soft and delicate, drying quickly when exposed to the air. They never completely surround the host roots, nor do they develop as large swellings as seen in *Gerardia* species when contact is made with the host. The original root tissues seem to fuse more intimately with the corresponding tissues of the host. Root hairs and root caps, as already noted by Smith (18, p. 113), were not found.

The radial arch-system is maintained, but the bundles are few in number; the small amount of xylem consisting of spiral tracheae and pitted vessels is poorly developed. The amount of phloem greatly exceeds that of the xylem, which is a feature we should expect to find in a holoparasitic plant whose chief object of parasitism is elaborated sap. The bundle system is surrounded by a pericambium and this in turn by a wide cortex of very large cells with abundant quantities of starch. No stone cells have been found in it. Surrounding the cortex is the epidermal layer. So intimate and complete is the connection made with the host roots that, epidermis of parasite is continuous with epidermis of host, cortex of parasite with cortex of host, etc., and were it not for the large cells of cortex with abundant contents as compared with the same tissue of the host, the line of demarcation between the two could scarcely be distinguished. In all this *Aphyllon* closely simulates species of *Orobanche* as figured by Koch (19).

As a still more condensed type *Christisonia* might well come next to *Aphyllon*. This is described and figured by Worsdell (20, p. 134). He describes three species of *Christisonia*, but the one that concerns us here is *Christisonia subacaulis*. To quote from him regarding it: "the most abnormal feature occurring in these plants is presented by the subterranean portion of *Christisonia subacaulis* especially, which, on investigation, is discovered to consist of organs having the character of roots, though their morphological nature is well concealed, owing to their extreme modification arising from their parasitic habit . . . The tubers, which arise at intervals in the root system of the plant just named, are the most important parts of it, for it is from these that the haustoria are chiefly formed, while they also act as reservoirs of nutriment for the whole plant . . . The haustorium is interesting as having an exogenous origin, and not an endogenous one, as described for many other parasites; it agrees in this respect with that of *Rhinanthus*."

The roots of *Epiphegus* are shorter than the roots of *Aphyllon* and seem to have lost all parasitic power, this function being accomplished by the tuberous swelling. A transverse section of such shows the host root deeply or shallowly buried within the tissues of the tuber and thus connection is established between the two. In these degradation stages the tissues of the parasite have become correspondingly more simplified as demonstrated by Cooke and Schively (17).

In *Conopholis* (Plate XVI, Fig. 32) no external roots are visible. With the more complete and highly specialized parasitism has come a complete absorption of roots, or they may be represented by a large mass of stone cells, but wholly buried within the enormous swelling on the oak roots. One specimen was found which measured 10 inches in length and 6 inches across. Sections were made of smaller specimens but these only showed masses of stone cells. All trace of definite systems seem to have been lost. And so, *Conopholis* well represents, both morphologically and physiologically, the climax of the entire group.

In summing up the discussion on roots it can be said that, beginning with *G. flava* and ending with the genus *Lathraea*, a gradual condensation in extent of root system is accompanied by a gradual degradation of root tissues which in *Lathraea* be-

come semi-woody, semi-fibrous. With this degradation parasitism becomes of increasing importance. Further condensation leads to *Orobanche* and *Aphyllon* with soft delicate roots and such is accompanied by further simplification in root tissues. From here the root system enlarges, becomes tuberous, and is characterized by an increasing degree of hardness of the tissues that reaches a climax in *Conopholis*. Further simplification of tissues here results in unintelligible interpretation.

Comparative Morphology and Physiology of Stem and Leaf

Under this heading stems and leaves will be considered. The drawings accompanying this part of the paper were made to illustrate more particularly relative lengths of stems.

In the most primitive Gerardias the stem is tall, well formed, and typically normal dicotyledonous, attaining a height of 1 to 4 feet in *G. flava* (Plate XIV, Fig. 9). The lower leaves are large, ovate-lanceolate, sinuate-toothed along the margins; in the upper leaves the margins are entire. Both stem and leaves are covered with a fine close down.

Transverse sections of the stem show a large pith area, a ring of xylem with numerous pitted vessels and internal to these spiral tracheae, a cambium, a narrow zone of phloem consisting of little soft and much hard bast. Externally the phloem is bounded by a cortex zone of 1 to 5 layers of cells, with the outer region collenchymatous and the inner region of thin-walled cells. The epidermis is persistent around the stem and from it project the numerous two to four-celled pointed hairs. The basal cell of these is large, rounded; the outer cells are narrow with the tip cell pointed.

G. purpurea, with stems 1 to 3 feet tall, has a comparatively small pith, but a wide zone of xylem. The phloem consists mainly of soft bast with occasional patches of hard bast. Sclerenchyma cells are a frequent feature of the cortex. The leaves of this species are much reduced in size, linear, acute, rough-margined according to Gray (21, p. 731). The rough character is due to many one-celled, pointed, more or less spiny hairs distributed over the general leaf surface and especially along the leaf margins.

In *G. aphylla* (Plate XIV, Fig. 10) a very marked condensation occurs. The stem is slender, rather wiry, unbranched, and from 6 to 18 inches in length. The leaves, much reduced in size, are scale-like, tapering almost to a point, and closely applied to the stem. Stomata are distributed over the leaf surface in comparatively small numbers when the entire foliage of the plant is taken into account. Leaves and stem are covered with short, conical, unicellular hairs.

Transverse sections of the stem taken at the same level as in the preceding genera are smaller in circumference. Stems tend to become quadrangular, being reinforced by scleroid cells at the angles. A rather wide green cortex surrounds the bundle system. Phloem consists of about equal amounts of hard and soft bast. Xylem is well developed and wide, enclosing a small pith area.

G. aspera (Plate XIV, Fig. 11) shows further reduction in height of stem. The internal structure is very similar to that of *G. aphylla*. Stem and leaves have hairs similar to those of *G. purpurea*.

Condensation advances even more markedly in *Harveya* and *Hyobanche* (Plate XIV, Fig. 12, 13) in that the stem is only from 4 to 6 inches in height. Both genera are parasitic, have scale-like leaves or these even reduced to functionless scales. Wettstein (22,p.97) describes *Hyobanche* as a fleshy low, parasitic plant with numerous scale-formed leaves, the lower scales being smaller than the upper ones. Material of this genus was not available for study, but the foregoing description regarding the fleshy nature of the plant suggests a very strong tendency toward genera of Orobanchaceae.

Transverse sections of the stem of *H. coccinea* have a wide pith around which the ring of bundles is arranged. These are more simplified than in the preceding genera, and in this respect *Harveya* is a good transition from species of *Gerardia* to *Orobanche* of the Orobanchaceae, in fact it is closer to *Orobanche* than to *Gerardia*. The xylem, while forming a continuous ring, is narrow in places and irregular; its elements are spiral tracheae and pitted vessels. The phloem is in excess of the xylem, soft bast of 1 to 3 layers of cells in patches, and hard bast that is very strikingly developed as 3 to 6 layers of cells forming a solid ring about the soft bast. The cortex is as wide as the phloem and xylem

combined and in places attains twice their extent in width; the cell walls show irregularity. The epidermis, from herbarium material, could not be described very accurately.

The hairs of *H. coccinea* are of special interest because of their large number, great size, and capitate-glandular character. They are distributed over both stem and scales; as many as 20 were counted around the edge of a cross section of the stem of reasonable thickness, which does not account for any that were broken off. The "stalk" of each hair consists of from 3 to 5 cells; the basal cell is usually short, broad, and rounded, while the others are elongated almost cylindrical; where two cells join, there is a collar-like constriction, giving the "stalk" the appearance of being jointed. The glandular tip is composed of 2 to 4 cells. Here again this genus is very similar to *Orobanche* which will be described later.

Proceeding from the last mentioned genus through the genera of Orobanchaceae the vegetative axes become more or less inconspicuous though enlarged fleshy (in some genera) and tuberous, and partly or wholly subterranean.

In the transition genus *Lathraea* (Plate XIII, Fig. 14) the vegetative axis has become a rhizome from 2 to 4 or 6 inches long, and is provided with the hollow scale leaves concerning which so much discussion has taken place, while from the annual short-lived inflorescence numerous flowers arise. The plant is described by Kerner (23, p. 135) as being destitute of chlorophyll. "The subterranean stems are white, have a fleshy, solid, and elastic appearance, and are covered throughout their entire length with thick squamous leaves placed closely one above the other." The leaves are broadly cordate. The scales being underground, naturally have lost their vegetative function, but are provided with cavities and structures for catching animal prey. Solereder (24, p. 586) says that the function ascribed by Kerner and Wettstein to these structures is incorrect according to Scherffel and Heinricher. Kerner describes two kinds of structures formed on the internal surfaces of the scale for which he suggests no special name in *Lathraea squamaria;* others have called them glands. One kind is composed of a cylindrical stalk cell and two cells forming a head, which project into the cavity of the scale; the other variety, which does not project into the scale, is composed of a tabular cell and two con-

vex cells, forming a low dome amongst the epidermal cells. The writer examined scales of *L japonica* and found similar structures projecting into the cavities of the scale. The cells of the epidermal tissues are from 4- to 6-sided and regular in outline. Stomata are either absent or present in small numbers; structures were found that had much the appearance of stomata, but no accurate statement regarding them could be made.

In the genus *Orobanche* (Plate XIII, Fig. 15) the vegetative axis is an inch and a half or less in length. If the rhizome of *Lathraea* be thought of as shortened and as a consequence the axis became tuberous and enlarged, the condition of affairs in *Orobanche* would be reached in which the stem axis is a shortened but enlarged tuber, covered densely with crowded scales. These are more elongated than the scales of *Lathraea*, e. g., in *O. minor*, broad oval at the base and lanceolate in their upper part; along the flowering axis they are lanceolate.

In *O. cruenta* the stem is exceptionally broad, measuring three-fourths of an inch across.

In transverse sections of the stem of *O. minor* their outline is found to be very irregular, which is due to some extent to the scales given off at different levels. There is however, irregularity also due to grooves and rather wide ridges, which become greater in number and more pronounced on the floral axis. Such sections show sections of the scales, as well, from whose outer surface are given off the glandular hairs, which agree in description with the hairs of *Harveya*. From 3 to 5 cells form a stalk with the capitate part of the hair of 2 to 4 cells. The cortex is unmodified, consisting of large thin-walled cells which are packed with starch grains. The bundle system consists of bundles arranged in an irregular manner about the pith area; phloem is next to the cortex and xylem next to the pith. The pith area is large and like the cortex has considerable starch in its cells.

Transverse sections of the flowering axis of *O. coerulea* show the irregularity in outline mentioned above to the greatest degree. The epidermal cells have heavy outer walls. The hairs are of the same type as for *Harveya* and *O. minor*, and are quite numerous. The cortex cells are thin-walled and have less starch than those of the stem cortex. The bundle system tends to become more loose and open than in the previous genera and

in places the bundles are separated; the amount of phloem is about twice that of the xylem and consists of hard and soft bast; the xylem has a few spiral tracheae and pitted vessels, that we best see in longitudinal sections.

The vegetative axis of *Aphyllon* (Plate XIII, Fig. 16) is reduced in thickness to scarcely more than one-fourth of an inch, or usually less, but in length is about one inch. The number of scale leaves is reduced to from 5 to 10, alternately placed and separated on the stem; they are smaller than the scales of *Orobanche* and decrease in size from the upper to the lower ones. The lower ones have neither stomata nor hairs, while the upper ones have both. The hairs are capitate and multicellular, like those of *Harveya* and *Orobanche*.

In making cross sections of the stem their soft and fleshy nature is at once recognized. The epidermis consists of small cells which are thickened on the free side; amongst these, stomata may be seen. The most conspicuous feature of the stem is the unusually large rounded thin-walled cells in the cortex and pith. Both regions are wide in extent and their cells are packed with large starch grains. Between these regions a comparatively narrow ring of bundles is arranged. The bundles are more widely separated than in *Orobanche*, thus making the medullary rays quite wide. Around the bundle system is a sheath of from 2 to 4 layers of cells, much smaller than the cortex cells and whose greater diameter is placed in a tangential direction. The excess amount of phloem over xylem is more pronounced than in the previous two genera. The phloem is external and xylem internal, the latter composed of a few spiral tracheae and pitted-reticulate cells.

Transverse sections of the flower stalk show the same arrangement of tissues as in the stem. The bundles are placed in a narrow ring about the pith and internal to the cortex; the xylem is slightly better developed than in the stem, while the phloem forms a continuous zone about the xylem. Cortex and pith have some starch grains. The epidermis, of small cells with free walls heavily thickened, is frequently interrupted by cells in groups of two slightly raised above its surface which appear to be stomata. Glandular capitate hairs, arising in great number from the flower stalk, have also two cells forming their base.

In *Epiphegus* (Plate XIII, Fig. 7) the vegetative stem and enlarged primary root tubercle become confluent into an oval

or rounded tuber from three-fourths to an inch and a half long. The writer considers the upper part of the tuber as the stem axis which bears the tooth-like scale-leaves. In some specimens the stem part consists of more than half of the tuber, in others of less than half. The scales are shorter, but more numerous than those of *Aphyllon*. Stomata are present on the scales, and along the scale-edge a few multicellular hairs were seen. Adventitious roots arise from the surface of the stem.

Histological details have been worked out by Cooke and Schively and the writer has found his own investigations to agree with their descriptions. But by way of comparison of this genus with preceding genera some of these details will bear repetition. The most notable feature is the bundle system, which becomes broken up into separate bundles that have no definite arrangement in rings, thus giving the stem a more loose and open aspect. This is an advance in degradation from *Aphyllon* in which the bundles, though separated, form a fairly definite ring about the pith. The phloem greatly exceeds the xylem, a further advance in degradation with increased parasitic habit. To quote shortly from Cooke and Schively: "The phloem of a bundle . . . . shows a tendency to spread out and lie in separate patches, while the xylem of each bundle seems always concentrated in a single area. Many of the bundles show an internal duplication with reversed order, phloem, xylem, xylem, phloem, succeeding each other from without inwards . . . An internal phloem is almost always present, often in excess of the outer phloem mass." No such state of affairs as the last exists in *Aphyllon*. As a consequence of the scattered and elongated bundles the cortex and pith areas have become reduced in size.

Sections of the floral axis have been described by others. The bundles are arranged in a ring. Considerable hard bast is developed. Hairs and stomata constitute the epidermal growths, the former showing considerable reduction in size as compared with the hairs on the floral axis of *Aphyllon*.

No definite statement will be ventured as to how much of the plant constitutes the stem axis in *Conopholis* (Plate XVI, Fig. 32). The aerial portion in its lower part is densely covered with scales that may represent reduced and degraded leaves, while slightly above this point the scales become more distinct, sep-

arated from one another, and increased in size, averaging 4 to 6 times the size of the lower ones. Sections made in the region of the crowded small scales show numerous patches of hard scleroid cells and the inner almost continuous ring of bundles, while in the position of the outer ring some fairly recognizable bundles are seen. Above this point the two rings of bundles become complete and the scleroid patches disappear; below this point the bundles become fewer in number and less recognizable, but the scleroid patches increase in number until in the tuberous part scleroid patches are the predominant feature and the bundles as such disappear. Evidently the lower part of the aerial portion represents a transition from stem axis to aerial shoot, and so, this part together with the upper part of the tuberous swelling might be considered as the stem axis. As in *Epiphegus*, stem system and root system have become confluent with no sharp line of distinction between the two.

Stomata have been reported absent from the scales but several were found on the lower or outer surface of the upper scales. From their shape they appear to be almost or quite functionless (Plate XV, Fig. 28). They are misshapen and poorly developed; some have two elongated guard cells which have slipped out of position and show a long orifice between them, others have three and four guard cells very loosely fitted together. Large multicellular and unicellular hairs are found on the edges of the scales which the drawings (Plate XV, Fig. 31) will sufficiently indicate.

The histology of the flowering axis is interesting for several reasons. The cortex and pith areas are quite large and consist of rounded cells of varying size and thickness with frequent large intercellular spaces. Some of the cells have contents while others are empty. Two definite rings of bundles surround the pith, which have a zone of fundamental tissue intervening. This quite agrees with Wilson's observations (25, p. 14) but disagrees with those of Chatin (26, p. 590) who says that *Epiphegus* and *Conopholis* have three rings. The majority of bundles in both rings are completely separated from each other by fundamental tissue, and this represents the climax in the series, beginning with *Harveya* in which the bundle system shows no tendency toward separation of bundles, thence to *Orobanche* which shows indications of such, thence to *Aphyllon* in which

the bundles show slight separation, thence to *Epiphegus* in which the bundle system is loose and broken up into separate bundles, which finally in *Conopholis* become still more widely separated and distinct.

As to the elements making up the bundles, the following is stated by Wilson (25): "Each bundle of the inner row has internally xylem, made of xylem cells and well-developed spiral tracheae. Next to the xylem is found the phloem, which in a longitudinal section proves to consist of both sieve tubes and companion cells. Adjacent to the phloem are a number of parenchyma cells, whose walls are so angular and so much thickened that in the photograph these bundles appear to be bi-collateral. That such is not the case, however, is easily proved on longitudinal section, when the parenchymatous nature of these cells is at once visible. Even in cross section, the color of the walls differentiates the wood from the thickened parenchyma.

The bundles of the exterior row have the same structure as those of the interior, only the xylem is now exterior so that the phloem masses of the two rows face each other."

Sections stained in safranin and methyl green also some in Delafield's haematoxylin and safranin bring out the bundle elements quite plainly. A different interpretation from the above, however, is suggested with reference to the arrangement of the elements of the bundle. Each bundle of the inner ring shows internally phloem, consisting of a large patch of hard bast and a patch of soft bast. The xylem comes next and is poorly developed, consisting of an interrupted line of cells, which are almost wholly large spiral tracheae, running across the bundle; in some bundles there are several rows of spiral tracheae and amongst them are several cells of phloem. Beyond the xylem is another small patch of soft bast and next to it another small patch of hard bast. The bundles of the outer ring show the same elements, but in reverse order, small patches of hard and soft bast, xylem, large patches of soft and hard bast.

Comparative Study of the Inflorescence

Regarding the inflorescence of the two supposed distinct families, several points are of special interest. In the parasitic Scrophulariaceae the flowering axes are elevated above the surface of the soil by the more or less elongated vegetative axes in

the less parasitic forms, but as these intervening vegetative axes become shortened and increasingly degraded in the more parasitic forms like *Harveya* and *Hyobanche* the flowering stalks gradually approach a lower level until they take their origin only a few inches from the ground. The conspicuous part of the plant then consists of the short vegetative axis and the floral axis. In the Orobanchaceae with the greatly reduced stems the flowering axes constitute almost wholly the aerial parts of the plant. In the former the flowering axes are woody, while in the latter they are more or less fleshy and stout, with one exception (*Aphyllon*).

The type of inflorescence for the Scrophulariaceae is given by systematists as centripetal, racemose. *Gerardia flava* has one floral axis along which short-pedicelled flowers are arranged racemosely. In *G. purpurea, G. aspera, G. aphylla* and others there are several floral axes, each of which constitutes a raceme; the pedicels are of varying lengths. In some of the more parasitic forms the branching of the flower stalk is less frequent and the flowers have very short pedicels so that the type of inflorescence tends to become a loose spike, e. g. *Orthocarpus purpurea, Euphrasia, Bartsia viscosa, Odontites, Hyobanche,* etc.

Aphyllon has one floral axis bearing a terminal flower. *Epiphegus* has branched flowering stalks and the flowers are arranged racemosely or in a spike. In the other genera, *Lathraea, Orobanche,* and *Conopholis,* of the Orobanchaceae the flowers are arranged in a dense spike.

The bracts of the flowers in Scrophulariaceae are leaf-like becoming scale-like, or even scales in *Hyobanche* while in Orobanchaceae they are scales.

Comparative Study of the Flower

Calyx.

The calyx in the different genera studied shows considerable variation in the number of sepals, in form, and in hairs.

In species of *Pedicularis* the calyx may be in the form of a funnel, or bell-shaped with from 2 to 5 teeth at the top. The teeth may be simple or further toothed or lobed.

The calyx of *Melampyrum lineare* is comparatively small and is made up of a short tube below and 4 tapering teeth above, the

teeth being longer than the tube. These are in pairs, with the upper pair slightly longer than the lower pair. Short, blunt, unicellular hairs and stomata are distributed over the surface of the calyx.

In *Bellardia* the calyx is much larger than in *Melampyrum*, and consists of the lower half of a bell-shape while the upper half is divided into 4 teeth. As in *Melampyrum*, the two lower teeth are about two-thirds the size of the upper ones. A prominent vein runs into each tooth. The hairs are numerous and of two kinds; very long, slender, unicellular, pointed hairs are found mainly along the edges of the teeth and prominent veins, and the less numerous 3- to 4-celled glandular hairs only along the main veins and edges of the teeth; while between the prominent veins they are almost wholly of the pointed type, but short and unicellular. Stomata are also present.

In *Fistularia* (*Alectorolophus* Bieb., *Rhinanthus* L. p. p.) the calyx consists of 4 sepals in pairs, the parts of which are united almost to their tips, but the pairs are separated for more than half of their length. Two sides of the calyx are pressed together in the young state, which in the fruiting stage become inflated and persistent around the fruit. Two types of hair are found on the surface; a short unicellular, and a long multicellular pointed type, also a glandular type with two rounded cells forming the top.

In species of *Gerardia* the bell-shaped calyx is 5-toothed, the teeth in most cases are shorter than the tube. In *G. purpurea* the teeth are very short to half the length of the tube and sharp-pointed. *G. flava* was referred to before as covered with a fine close down, which character applies to the calyx as well. A peculiar feature of the hairs in this species is the spiral thickenings found in them. The short pointed type is rare or wanting entirely. In *G. aspera* and *G. purpurea* the short, pointed hairs are the predominant type; these are both one- and several-celled. The latter has also short glandular hairs. Stomata are a common feature in the three species. The epidermal cells are regular in outline.

In *Euphrasia americana* the calyx is small, 4-toothed, the teeth being longer than the tube and lanceolate. Pointed unicellular hairs are quite common, but are not found all the way to the tip of the calyx teeth. The short glandular hairs are con-

fined largely to the angles formed by the bases of the calyx teeth. The former type is roughened along the margins. Epidermal cell walls are wavy.

Bartsia alpina has a relatively large calyx of 4 parts, with the teeth about as long as the tubular part. Long-stalked glandular hairs are abundant; the stalk consists of 3 to 6 slender cells, while the top of it has from 2 to 5 cells arranged in parallel rows. Pointed multicellular hairs, though present, are few in number. Epidermal cells are irregular in outline.

In *Harveya* the tubular part of the calyx is short and the 5 lobes extend almost to the base. As already described in connection with the stem histology, the hairs are of maximum size and wholly glandular. The stalk cells are comparatively wide and stout, are 3 to 6 in number, and capped by the gland cells. Unlike the majority of the genera already described, the hairs in this genus fringe the edges of the sepals.

Hyobanche has a calyx of 5 parts which are almost distinct and more rounded than in *Harveya*.

Among the Orobanchaceae similar variation may be seen in the calyx, as in Scrophulariaceae. According to Le Maout and Decaisne (27, p. 593) the "calyx is persistent, tubular or campanulate, 4-5 fid, or of 4 sepals more or less completely united in lateral pairs."

In species of *Orobanche* variation occurs, for the calyx may be split both above and below, nearly or quite to the base; the divisions may be 2-cleft or entire, or more or less unequally 2- to 5-toothed. In *O. coerulea* and *O. minor* the teeth are about as long as the tube, and are lanceolate-subulate. The hairs on these two species are similar to those of *Harveya* but smaller.

The calyx of *Epiphegus* is small, the teeth very much shorter than the tube below. Cooke and Schively (28, p. 377) state the following concerning hairs: "One-celled, rarely two-celled hairs fringe the edges of the lobes. Below, across the base of the lobes, there extends a band of two or three-celled hairs, longer than the upper hairs. All of these hairs are on the outer surface of the calyx; none are present on the inner surface. They have a swollen granular appearance." The writer has found his own descriptions to agree with the above.

In *Lathraea* the calyx is bell-shaped with 4 to 5 rounded teeth above.

The calyx of *Aphyllon* is 5-toothed, the teeth equal to, or longer than the tube. Glandular hairs are numerous and distributed over the entire outer surface of the calyx; shortly, these consist of a short broad basal cell, then a long cylindric cell, next to this 2 to 3 cells decreasing in size, and finally the top or capitate part of several rounded cells. Stomata are numerous and of the normal type.

In *Conopholis* the calyx is orbicular, split in front, and toothed at the tip. Hairs and stomata are negligible in this genus.

Stamens.

The stamens in parasitic Scrophulariaceae and Orobanchaceae are 4, didynamous, in Gesneraceae, 5 to 4 to 2.

As to anthers, a totally different relation holds between parasitic Scrophulariaceae and Orobanchaceae on the one hand as compared with Gesneraceae on the other. In the former the top of the filament is broadly inserted into the swollen back of the anther, the lobes of which in the parasitic Scrophulariaceae and Orobanchaceae are prolonged above the connections, but in a striking manner are prolonged downward as two parallel or divergent awns. These anther lobes in all except two genera of Scrophulariaceae (*Harveya*, *Hyobanche*) and two genera of Orobanchaceae (*Campbellia*, *Aeginetia*) are like each other, that is, are equally paired anther lobes. But in *Harveya* one anther lobe is large, normal, and polleniferous, and prolonged below into a long horn; the other lobe is small, abortive, and radiates back from the top of the filament. The latter anther lobe in *Hyobanche* has been entirely absorbed, so that now one fertile anther lobe dehisces by a single basilar pore.

It is of interest to find that in *Christisonia* and *Aeginetia* of the Orobanchaceae a similar structure exists, for, as in *Hyobanche* and *Harveya*, each bears a single fertile anther lobe.

As to antherine structure, this exactly agrees in parasitic Scrophulariaceae and Orobanchaceae and totally differs from anything encountered in Gesneraceae. The structure and appearance of such genera as *Melampyrum*, *Tozzia*, *Euphrasia*, *Pedicularis*, *Buchnera*, *Gerardia*, *Bartsia*, etc., absolutely resemble those of Orobanchaceae, and this the writer would regard as one of the most important points of contact between the two families.

The anthers in the various genera of the Gesneraceae conform to a totally different type from that shown alike in Scrophulariaceae and Orobanchaceae. In the former, when the flowers become nearly or quite regular as in cultivated varieties of *Gloxinia* and also in species of *Streptocarpus*, as well as in other genera, the anther lobes are adpressed at their tips and cohere so as to form a solid antherine box. When the flowers are irregular, as in nearly all members of the family, the 4 anthers are pressed together in pairs by their tips. In the entire group further, the bases of the anthers are either parallel and with blunt rounded extremities, or the anther lobes diverge in their lower part but are blunt and rounded in their divaricate bases. In no case studied by the writer is there any indication of the anther lobes being arranged in parallel pairs that at their lower extremities become prolonged into horned or horn-like awns. This peculiarity is typical, as will be traced, in most of the known parasitic Scrophulariaceae and directly continued as a character to the Orobanchaceae.

Of all the genera examined *Gerardia flava* might well be placed at the top of the list regarding the size of its anthers. As illustrated in Plate XV, Fig. 17, the anther lobes are large, elliptical, rounded at the upper extremities and at their lower extremities are projected abruptly into two long tapered, somewhat divergent processes. The front and sides of the anthers are covered with numerous long, multicellular hairs. These are present also on the filaments.

The anthers of *G. purpurea* (Plate XV, Fig. 18) are smaller and taper more gradually downward into processes that lie almost parallel with each other. The filament is inserted above the middle of the anther lobes. Anthers and fllaments are hairy.

In *G. aphylla* (Plate XV, Fig. 24) and *G. aspera* the processes are relatively short and less pointed than in the former species. Both anthers and filaments are covered with hairs.

In *Melampyrum lineare* the anthers agree fairly well with those of *G. purpurea*, but are smaller. Along the filaments knob-like swellings of 1 to 2 cells are seen.

The antherine condition of *Harveya* is set forth in Plate XV, Fig. 19 and has already been referred to.

Other genera of Scrophulariaceae like *Bartsia* (Plate XV, Fig. 20) *Tozzia*, *Bellardia*, show likewise the downwardly-directed anther-processes.

For *Lathraea squamaria* Kerner figures basal anther-processes similar to those in the above genera.

The stamens of two species of *Orobanche*, also those of *Aphyllon*, *Epiphegus* and *Conopholis* are figured in Plate XV, Figs. 25, 26, 27, 23, 22, all of which have the downwardly-directed processes.

In *Orobanche coerulea* the anther lobes are round above and taper gradually downward into rather short processes at their lower extremities, which are slightly convergent.

In *O. minor* the shape of the anther lobes is approximately rectangular, with the processes given off from the sides next to the filament.

In *Aphyllon* the anthers are comparatively small. The filament is inserted above the middle of the anther lobes, with the processes at their lower extremities.

Hairs on the stamens are a constant feature in all the above.

The parasitic Scrophulariaceae and Orobanchaceae thus have a character in common. Further, this character becomes more important when the function of the processes is considered, for in both groups these are contrivances designed to aid in the shedding and dissemination of the pollen grains. With regard to the genus *Bartsia*, Knuth (29, p. 229) says of *B. apula* the following: "In this Dalmatian species each anther possesses a downwardly-pointing process, which is pushed to one side by insects, thus opening the pollen receptacle and causing pollen to be sprinkled on the head and back of the visitor."

In connection with the description of pollination in *Lathraea squamaria* the statement is made by Knuth that the pollen can not fall out until the short, blunt point of an anther receives a blow from an insect. Again, under species of *Orobanche* the following is stated: "The four anthers are laterally united, and each lobe is provided with a sharp, stiff, downwardly-directed process. These processes are behind the stigma, and if anything strikes against them the bright-yellow, powdery pollen falls out of the anther-lobes, and is sprinkled on the proboscis or head of the visitor."

Histologically the structure of the awns shows a striking agreement throughout the genera of Scrophulariaceae and Orobanchaceae already mentioned, in that as one passes from each anther lobe toward their downwardly-directed awns the epider-

mis or exothecial tissues become increasingly thickened on their outer and lateral walls in u-shaped manner until toward the tip of each awn the thickening may be almost as deep as the cell cavity. Transverse and longitudinal sections of the awns of *Aphyllon* are figured in Plate XV, Figs. 29, 30.

Were the above not a continuous morphological series from green to degraded parasitic plants, one can scarcely suppose that such similarities and histological details could have evolved in two such related families.

Pistil

In a study of the pistil the fundamental point for consideration is the supposed invariable two-celled ovary in Scrophulariaceae and the one-celled ovary in Orobanchaceae and Gesneraceae. This has already been discussed generally on pages 6–8. The varying structural details from a two- to one-celled condition, as well as the diverse views expressed as to the affinities of such genera as *Hyobanche, Lathraea, Christisonia* that show wavering transition from two- to one-celled states, emphasize again the fact that here we are dealing with a condensing and simplifying variation. No such transition-relations are even suggested between Gesneraceae and Orobanchaceae.

In the different genera of the Orobanchaceae the fused margins of the carpels grow inward to a varying degree from shallow marginal placentas to deep parietal, that approach central placentation. So the fundamental point of supposed affinities between Gesneraceae and Orobanchaceae entirely breaks down, while a natural and continuous affinity between degraded parasitic Scrophulariaceae and still more degraded Orobanchaceae has been established.

Hairs of the Pistil

The presence of hairs on the style and ovary in the different genera of the two families is not a constant feature. They differ as to number, distribution, and type. The following results were noted:

In *Gerardia aspera* the hairs on the style, though present, are few in number.

In species of *Odontites* the base of the style and upper part of the ovary are very hairy, while the upper part of the style is almost glabrous. The hairs are long, narrow and pointed.

In *Rhinanthus* the hairs are numerous from the stigma downward but decrease in number toward the base of the style and finally disappear. They consist of one cell pointed at the distal end on the upper part of the style, and of 2 to 3 cells on the lower part of the style, and are broad at the base, tapering gradually toward the tip.

In *Bartsia alpina* the numerous one- to several-celled hairs are distributed along the entire style and the upper half of the ovarian surface, being most numerous on the ovary. They are quite long and needle-like in appearance.

In *Bellardia* they are exceedingly numerous along the entire stylar surface, and consist of one needle-like cell that is dark in color.

In *Orobanche coerulea* the glandular type of hair is seen along the entire style, similar to the hairs found on other parts of the plant already described.

The style and ovary in the genera *Aphyllon*, *Epiphegus* and *Conopholis* are glabrous, although the stigmatic areas of the first two mentioned are covered with comparatively short unicellular hairs.

The Nectary

The nectary of Scrophulariaceae is described by Wettstein (30, p. 39) as hypogynous, ring formed or one-sided. Beck (31, p. 127) gives a similar description for Orobanchaceae. "Nektar absondernden Stellen am Grunde der Stf. oder am Grunde des Frkn. ringförmige, oft buckelig, seltener beutelförmig vorspringende Nektarien." For Gesneraceae Fritsch describes the nectary as a "Discus" usually well developed, ring to cup-shaped, or as reduced isolated glands, which may be also one-sided. While these general descriptions fairly agree in the three families, mostly one-sided nectaries are characteristic of parasitic Scrophulariaceae and Orobanchaceae, as will now be taken up.

In *Melampyrum pratense* "the nectary expands toward the lower lip into a whitish rounded body, on either side of which runs a nectar-secreting groove."

In *M. lineare* the nectary consists of a similarly rounded body placed to one side of the ovary.

The general description of the nectary for *Rhinanthus* is given by Knuth. He says that nectar is secreted by the fleshy base

of the ovary which projects to the front, and it is stored in the bottom of the corolla tube. In all the species examined by the writer the nectary agrees with this description, but further, it is curved inward at the top and points directly toward the ovary as a tongue-like process.

In *Bartsia alpina* the nectar is secreted by a cushion-like swelling at the lower side of the base of the ovary, extending a little beyond as a rounded knob.

Lathraea squamaria has a large, roundly triangular and somewhat lobed nectary situated at the base of the ovary.

In *L. clandestina* the ovary is laterally compressed and traversed bv a longitudinal groove, bearing in front a three-lobed nectary.

One species of *Orobanche, crenata,* "secretes nectar at the orange-yellow base of the ovary."

The nectary of *Aphyllon* is a small, rounded, whitish swelling at the base and a little to one side of the ovary.

In *Epiphegus* the nectary appears as a swelling on one side of the ovarv, antero-laterally in position, just above the base.

The nectary of *Conopholis* is a rudimentary ovarian gland.

The Seeds

The seeds vary in number from 4 in one capsule of some genera of the Scrophulariaceae, (*Melampyrum, Rhinanthus*) to very numerous (as many as 1500 in one capsule) in other genera of Scrophulariaceae and Orobanchaceae. Increase in seed number is usually accompanied by a reduction in size, so that the seeds become very small in such genera as *Epiphegus* and *Aphyllon.* In structural details, the seeds of the purely parasitic genera are simplified and most degraded; in some of them the embryo consists of a small group of undifferentiated cells (*Aphyllon, Epiphegus.*)

To supplement the writer's information, gathered from his own examination of material, Bentham and Hooker's "Genera Plantarum" (32, pp. 967–980) was used as the chief source for genera of Scrophulariaceae.

The seeds of *Rhinanthus* are few in number, sub-orbicular, compressed, and surrounded by a wing-like structure. The embryo is small.

Melampyrum has from 2 to 4 seeds which are smooth, and have an aril-like appendage at the base.

In *Gerardia*, the seeds are numerous, oblong wedge-shaped or angular; the testa is loose-fitting.

In *Euphrasia*, the numerous seeds are pendulous, oblong, with longitudinal ridges.

In *Bartsia*, the seeds are many, pendulous, or may be numerous and placed subtransversely, with wings and longitudinal ridges.

In *Tozzia*, the seeds are ovoid-globose; the testa is appressed; and the embryo is small.

The seeds of *Buchnera* are very numerous and ovoid or oblong; the testa is reticulate, subappressed.

In *Harveya*, the seeds are very numerous; the testa is heavily reticulated and loose; the embryo is equal to half the albumen in amount.

In *Hyobanche*, the seeds are numerous, small, globose; the testa is loose, reticulated.

Lathraea has numerous small seeds, spherical in shape, and the testa is wrinkled.

In species of *Orobanche*, the seeds are numerous, reticulated, wrinkled or striate; the embryo is minute with cotyledons scarcely differentiated.

In *Christisonia*, the seeds are extremely numerous, very small, and subglobose, and the testa is reticulated.

In *Aphyllon*, the seeds are numerous, small, light, surrounded by a tough leathery coat of flattened cells with thick indurated walls; the endosperm cells are filled with starch and enclose a small embryo consisting of a group of undifferentiated cells.

In *Conopholis*, the seeds are of fair size, numerous, and somewhat quadrangular in shape; the embryo is small, undifferentiated; and the testa is heavily thickened.

In *Epiphegus*, the seeds are very numerous (from 700 to 1800) small, oblong in shape; the embryo is a group of undifferentiated cells; and the testa cells are elongated with much thickened walls.

Selection of Hosts

The less parasitic Scrophulariaceae have a rather wide range of hosts. The species of *Gerardia* parasitize on Grasses, Composites, etc., as has already been stated.

For *Bartsia*, the following are given as hosts: *Avena flavescens*, *Phleum pratense*, *Trifolium pratense*.

Tozzia parasitizes on the roots of *Ranunculus*, *Petasites*, *Rumex*, and *Alchemilla*.

Poa, *Avena*, *Luzula*, *Carex*, *Senecio*, *Trifolium*, *Capsella*, *Epilobium*, and *Festuca*, are given by Heinricher as hosts of *Euphrasia*.

The roots of *Lathraea* may attach themselves to the roots of Ash, Elm, Poplar, Hornbeam, and Hazel as hosts.

Species of *Orobanche* seem to have a very wide range of hosts. According to Koch (16), *Orobanche minor* may parasitize on 44 species of plants; *O. ramosa* on 29 species; *O. speciosa* on 13 species, and *O. hederae* on 3 species. These hosts may be found amongst members of Papilionaceae, Geraniaceae, Cruciferae, Oleaceae, Ranunculaceae, and others.

Although various species have been given as hosts of *Aphyllon*, the writer quite agrees with Smith in finding it to grow only on the roots of *Aster corymbosum*.

Epiphegus has been found to grow only on the roots of *Fagus americana*. *Conopholis* similarly parasitizes on but the one genus *Quercus*, and so far as the writer has learned on the group of the red oaks.

The writer feels deeply indebted to Professor John M. Macfarlane who first suggested the work and whose valuable criticisms, and assistance have been a source of constant encouragement in the preparation of this paper. Thanks are due to Mr. W. R. Taylor for the photographs in Plate XVI, to Dr. F. W. Pennell for the use of several slides, and to Mr. H. W. Stout for locating a growth of *Conopholis*.

Summary

A short review of the evidences dealt with above might be put in summary form as follows:

1. All macroscopic and microscopic details suggest that the parasitic Scrophulariaceae and Orobanchaceae form a continuous and parasitically degrading morphological series that show transitional steps from green nearly autotrophic plants like *Melampyrum*, *Rhinanthus*, and *Euphrasia* to increasingly condensed and degraded genera like *Bartsia* and *Harveya*, on to *Lathraea*, that has been shown to be placed by some botanists in *Scrophulariaceae*, by others in Orobanchaceae, thence through species of *Orobanche* to *Epiphegus*, and finally *Aphyllon* and

Conopholis. No such continuity exists between the wholly green autotrophic Gesneraceae and Orobanchaceae, nor are any members of the Gesneraceae parasitic.

2. During progressive parasitism in Scrophulariaceae and Orobanchaceae commencing parasitism consists in a few of the fibrous roots becoming enlarged toward their extremities into parasitic haustoria, while other roots are still autotrophic in relation. With increasing parasitism these secondary roots become shortened and the primary root also condenses into a central knob or swelling as can be traced successively in *Gerardia*, *Lathraea*, *Orobanche*, *Epiphegus*, *Conopholis* and *Aphyllon*. Ultimately, complete vegetative fusion and enlargements between primary root and ascending vegetative axis result in the formation of a rounded tuber (*Epiphegus*) or greatly swollen rounded or oval mass (*Conopholis*) difficultly distinguishable from the enlarged roots of oak on which the last grows.

3. In progressive degradation the elongated ascending leafy axis of *Gerardia* or *Bartsia* shortens steadily, and in *Harveya* and *Hyobanche* becomes a short axis bearing reduced nonchlorophylloid foliage leaves. These are seen in *Lathraea* to become the characteristic scales investigated by numerous observers. In *Orobanche* the leafy axis is reduced to a short tuber that is separated from the condensed primary root by a constricted neck (*O. cruenta*), or the primary root and scaly axis become continuous as in *O. minor*. This by progressive degradation becomes a slightly constricted root part below and a stem part above, covered by tooth-shaped leaf-scales, or an oval tuber only, that is primary root below and tooth-scale stem above (*Epiphegus*). In *Conopholis* even this distinction is largely obliterated.

4. In the less parasitic types, e. g., *G. flava*, the leaves are large green and actively vegetative, but by gradual stages become in time small and scale-like in *G. aphylla*. In *Harveya* and *Hyobanche* they are scattered along 2 to 6 inches of the condensing axis. In *Lathraea*, these scales are largely underground colorless, or purplish-white, and extend over 1 to 3 inches of the vegetative shoot. In *Orobanche* the brown, yellow or red scales cover the short tuberous vegetative axis for one to one-fourth of an inch. The same is true for *Epiphegus*, or the scales are rather shorter for *Aphyllon*. In *Conopholis* the intimate fusion

of root and vegetative axis has resulted in practical obliteration of any distinction of parts.

5. The inflorescence axis from being greatly elongated to constitute a several- to many-flowered raceme becomes a relatively simplified axis with a reduced number of flowers, the climax of which is reached in *Conopholis*, which bears a spike with 40 to 10 flowers. In *Aphyllon* each inflorescence is represented by a single flower.

6. It has been shown that the histological details, of stem and leaf in the above progressive series of degrading parasitic types, agree fundamentally with and verify the naked eye characters.

7. The sepals of Scrophulariaceae and Orobanchaceae have been found to show fundamentally similar structures and at times to show similar condensation in the former from a five-leaved to a four-leaved calyx through absorption of the odd sepal, as in *Tozzia*, *Euphrasia* and others. *Lathraea*, as an intermediate type, may have a five to four-lobed calyx, and finally, species of *Orobanche* and *Boschniakia* may show five to three sepals making up the calyx.

8. In structure the stamens have been shown to constitute an important link in the chain of evidence, for in all Gesneraceae the anther lobes more or less converge and press against each other at the apex and are rounded, as well as often divaricate at their bases. In Scrophulariaceae and Orobanchaceae the macroscopic and microscopic details proclaim progressive modifications in that the bases of the parallel anther lobes grow downward into stiff awn-like horns, whose terminal cells are similarly thickened throughout the series, and show a similar mode of unequal thickening. In pollination, therefore, authors like Ogle, Müller, and Knuth demonstrate similar pollination arrangements for Scrophulariaceae and Orobanchaceae that differ markedly from those in Gesneraceae.

9. Histologically, the sepals and stamens have been shown in many of the types to bear tapered multicellular hairs interspersed with capitate-glandular hairs that suggest strongly an origin in common.

10. The nectary in Gesneraceae is a cylindric structure that appears either as a simple girdle, or as a series of connected nectariferous knobs; very rarely is it a median unpaired swelling. In Scrophulariaceae and Orobanchaceae the nectary is

often a median knob in line with the antero-posterior axis of the flower, or somewhat displaced.

11. Evidence has been given to show that while the ovary is two-celled in Scrophulariaceae and usually one-celled with deep to shallow placentas in Orobanchaceae, all transitions between these can be traced from *Harveya* and *Hyobanche* to *Lathraea clandestina* and *Christisonia albida*, etc.

12. As to seeds, these are few (4–12) and fairly large in the less parasitic Scrophulariaceae, becoming decidedly small and numerous in *Harveya* and allied types of Scrophulariaceae as well as in all of the Orobanchaceae.

13. In structural details and morphological complexity the seeds show continuous degradation changes from the less parasitic genera of Scrophulariaceae to the most degraded genera of Orobanchaceae, such as *Aphyllon* and *Conopholis*, in which a rudimentary endosperm and formless embryo are alone developed up to the time of germination.

14. Physiologically it has been shown that in transition from the less parasitic Scrophulariaceae, like *Odontites* and *Gerardia* which parasitize on a variety of hosts, transitions are shown to genera like *Orobanche*, some species of which seem to confine their parasitism to the species of a family or even to the species of a genus, as pointed out by Beck (p. 31), while finally in such a highly degraded type as *Epiphegus* abundant evidence shows it to be purely parasitic on *Fagus americana*, *Aphyllon* to be similarly wholly parasitic on *Aster corymbosum*, and *Conopholis* on one or two species of *Quercus*.

Conclusions

From a review of the above observations, the writer believes that ample evidence has been adduced to show that direct and distinct continuity can be established from non-parasitic through semi-parasitic Scrophulariaceae to the most degraded parasites of the family, and that these again show direct continuity with the still more degraded and condensedly parasitic types of Orobanchaceae.

Alike logically and biologically, therefore, the two types should be treated in continuous descending series from the highest to the most degraded genera.

EXPLANATION OF PLATES.

Key to the lettering of Figures 1–16.

r—The primary root from which are given off secondary rootlets.
st—Stem.
hr—Host root
fl—Foliage leaf.
fs—Foliage scale.
i—Inflorescence axis.

PLATE XII.

Fig. 1. Root system of *Gerardia flava* showing parasitic attachment. (From a drawing by Mr. J. Stauffer in Gray's "Structural Botany.")
Fig. 2. Root system of *Gerardia purpurea*. Natural size.
Fig. 3. Root system of *Gerardia aphylla*. Natural size.
Fig. 4. Root system of *Orobanche minor*.

PLATE XIII.

Fig. 5. Root system and part of stem of *Orobanche minor* attached to clover root. (After Koch).
Fig. 6. Stem and root system of *Aphyllon uniflorum* parasitic on the roots of *Aster corymbosum*. Natural size.
Fig. 7. Tuberous swelling consisting of stem and root system of *Epiphegus virginiana*. Natural size.
Fig. 8. Stem and root system of *Orobanche cruenta* with constricted neck at the junction of stem and root. Natural size.
Fig. 14. Root, underground stem, and lower part of inflorescence axis of *Lathraea japonica*. (× ½).
Fig. 15. *Orobanche minor*. Note the short condensed stem, from *i* downward, as compared with that of *Lathraea*. (× ½).
Fig. 16. *Aphyllon*. Stem still more condensed and shorter than that of *Orobanche*. (× ½).

PLATE XIV—Note the gradual condensation and shortening of stem in Figs. 9–13. Foliage leaves become scales.
Fig. 9. *Gerardia flava*. (× ¼).
Fig. 10. *Gerardia aphylla*. (× ¼).
Fig. 11. *Gerardia aspera*. (× ¼).
Fig. 12. *Harveya capensis*. (× ¼).
Fig. 13. *Hyobanche*. (× ¼).

PLATE XV—Figures 17–27 show the downwardly-directed processes at the base of the anther lobes. (× 10).
Fig. 17. Stamen of *Gerardia flava*.
Fig. 18. Stamen of *Gerardia purpurea*.
Fig. 19. Stamen of *Harveya coccinea*. Note the elongated sterile anther lobe.
Fig. 20. Stamen of *Bartsia*.
Fig. 21. Stamen of *Melampyrum*.

Fig. 22. Stamen of *Conopholis*, front and back views.
Fig. 23. Stamen of *Epiphegus*, front and back views.
Fig. 24. Stamen of *Gerardia aphylla*.
Fig. 25. Stamen of *Orobanche minor*.
Fig. 26. Stamen of *Orobanche coerulea*.
Fig. 27. Stamen of *Aphyllon uniflorum*, front and back views.
Fig. 28. Epidermal cells and stomata on a scale of *Conopholis*. (× 115).
Fig. 29. Transverse section of the awn-like horn at the base of an anther of *Aphyllon*. The epidermal tissue shows cells with the outer and radial walls much thickened in u-shaped manner. (× 115).
Fig. 30. A longitudinal section of the awn-like horn of an anther of *Aphyllon*. (× 115).

PLATE XVI.

Fig. 32. Aerial flowering shoots of *Conopholis* showing attachment at the base to the swelling on the oak root. Originally there were 40 shoots growing from the one swelling. (× ½).
Fig. 33. Tuberous swelling on oak root showing the numerous excrescences from which the flowering shoots arise. (× ⅓).

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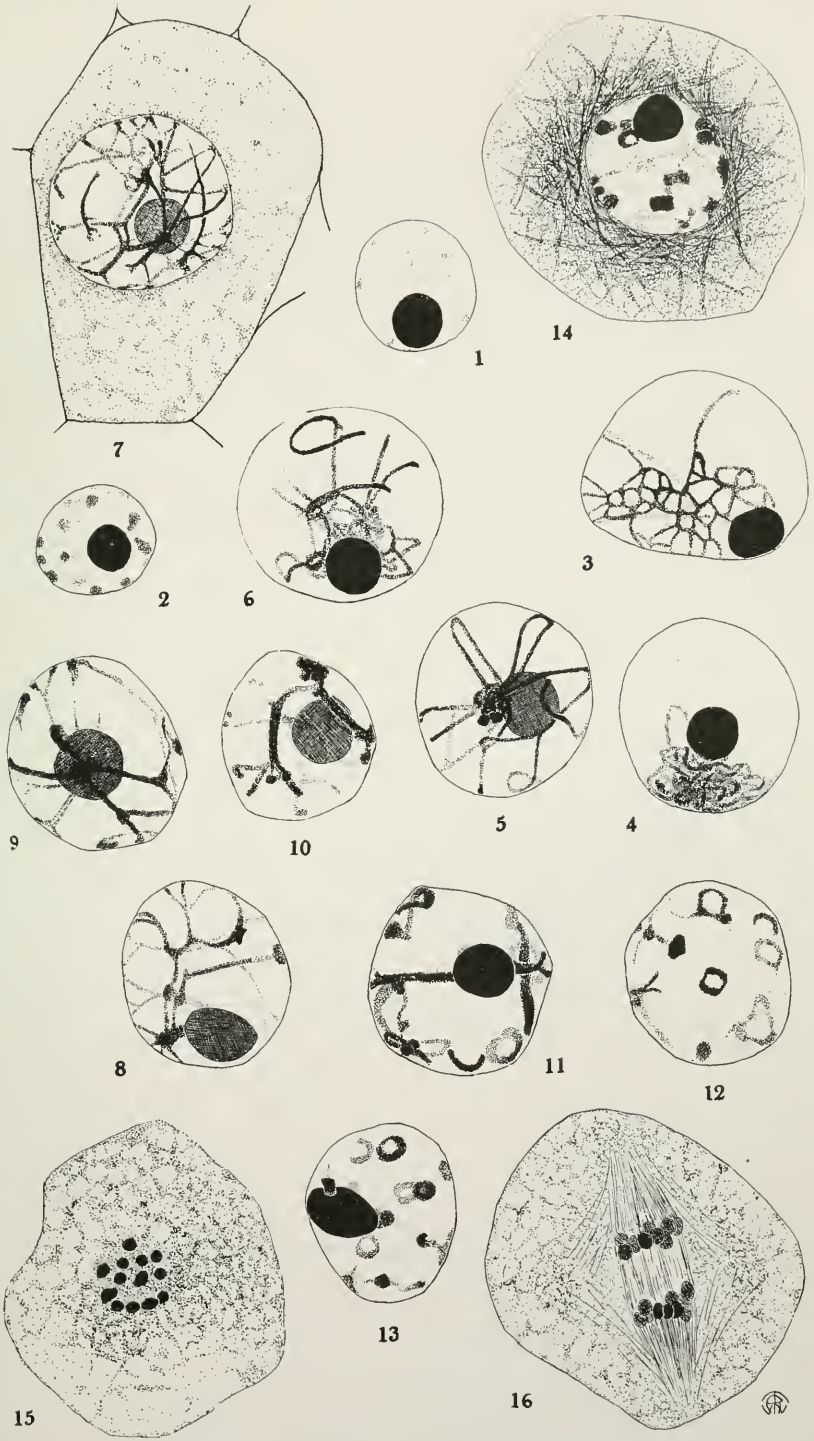

TAYLOR ON REPRODUCTION IN ACER.

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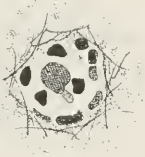

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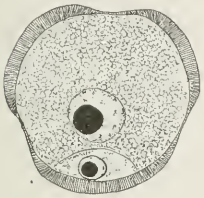

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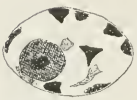

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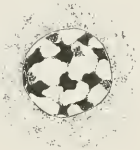

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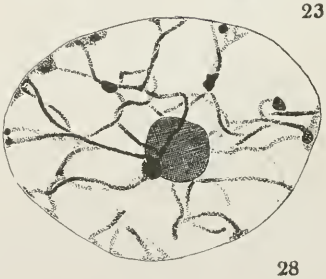

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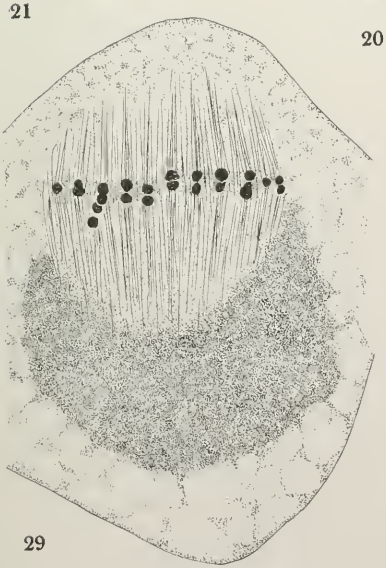

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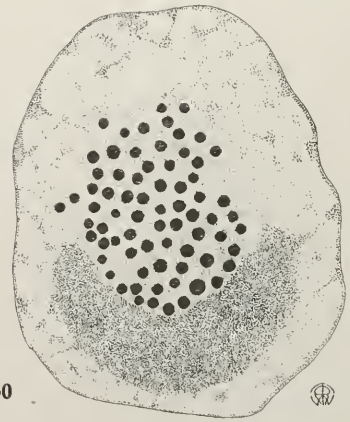

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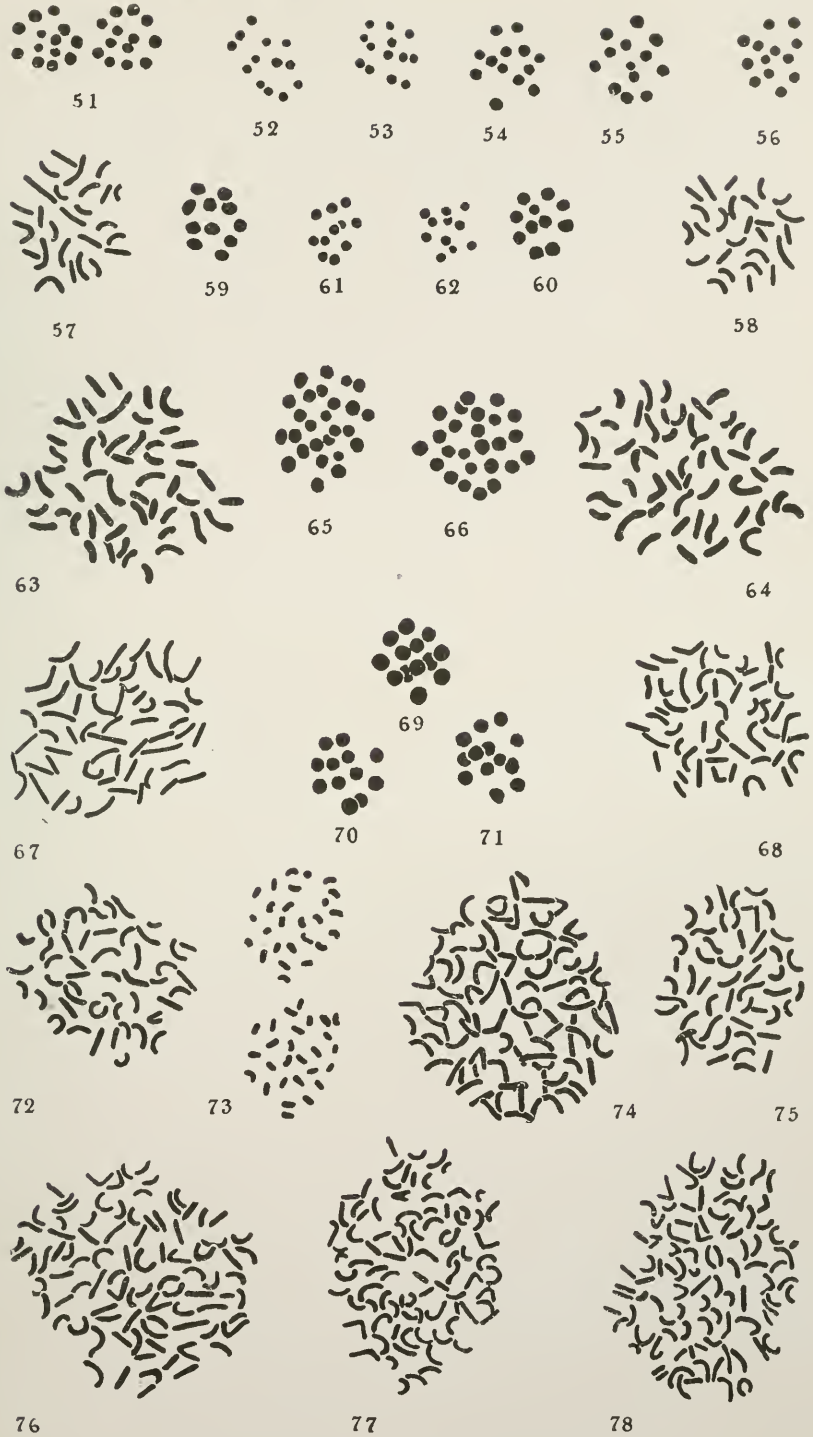

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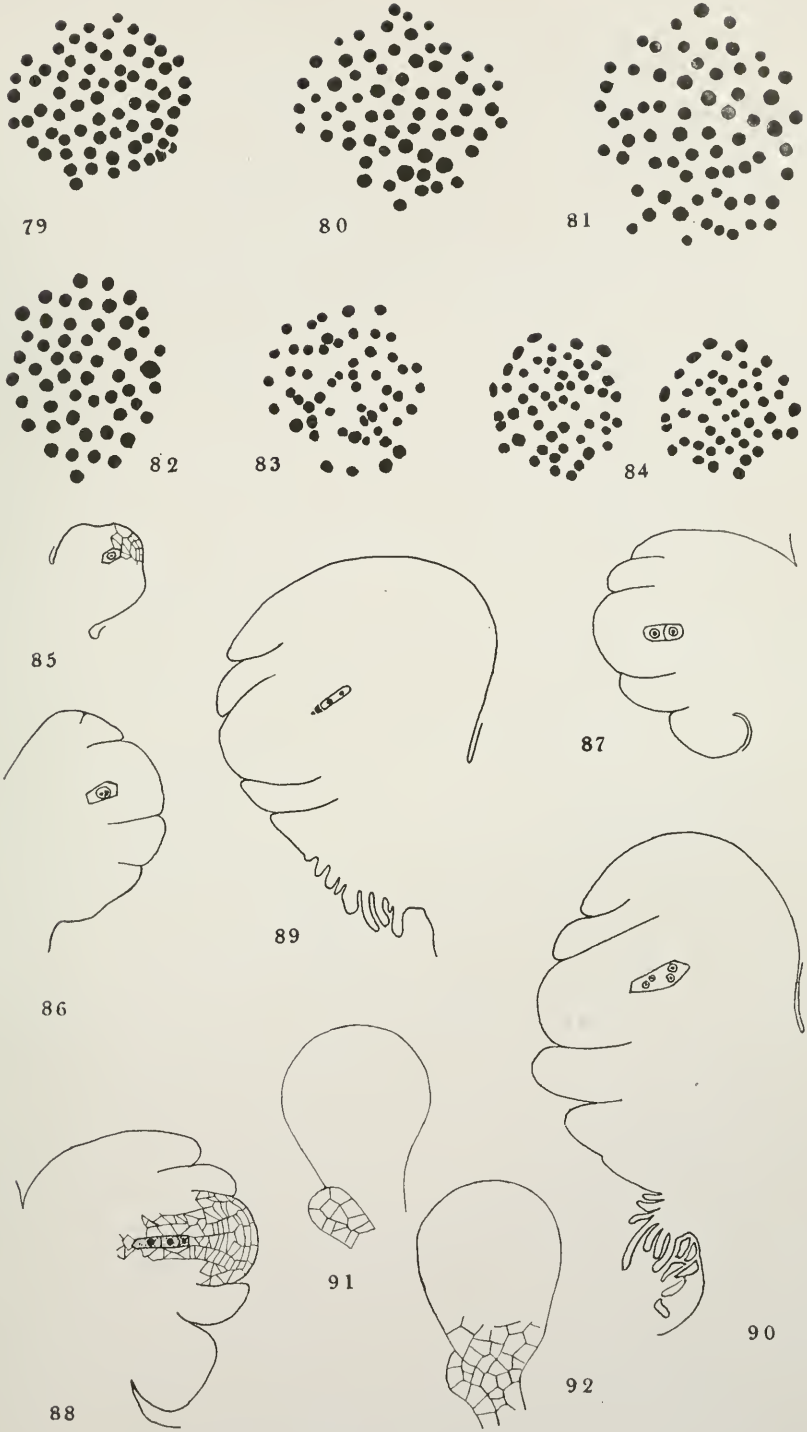

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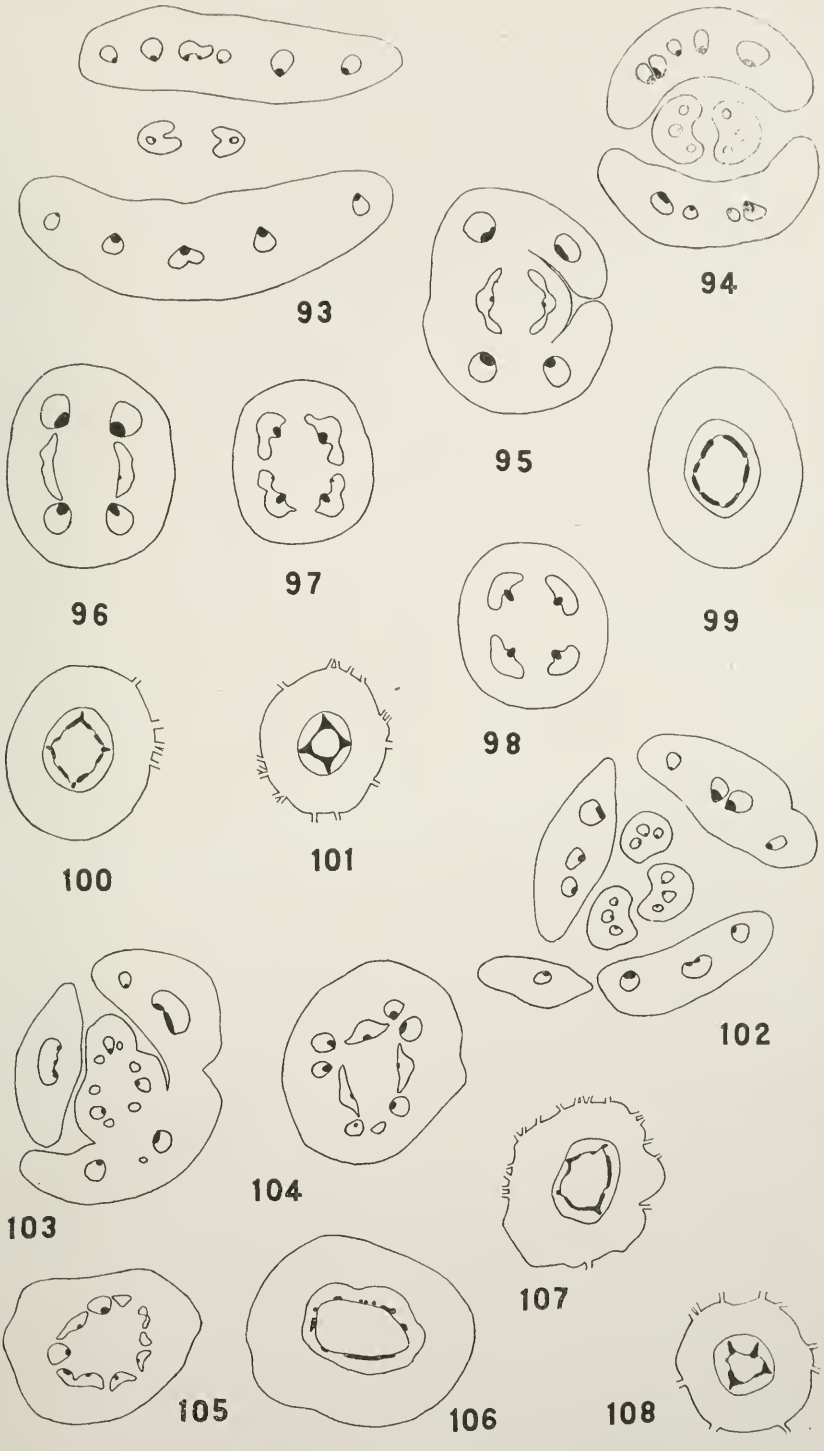

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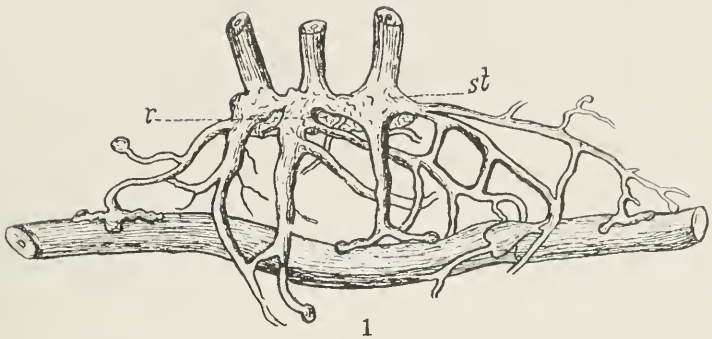

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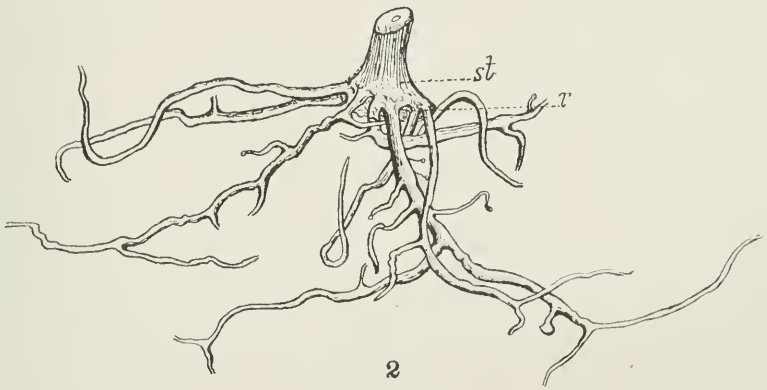

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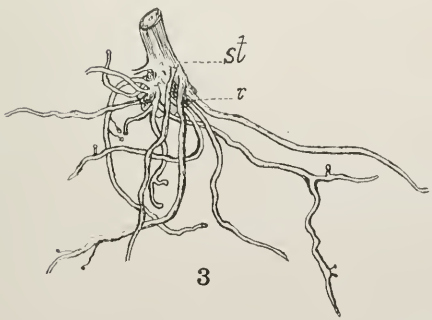

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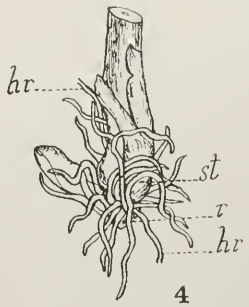

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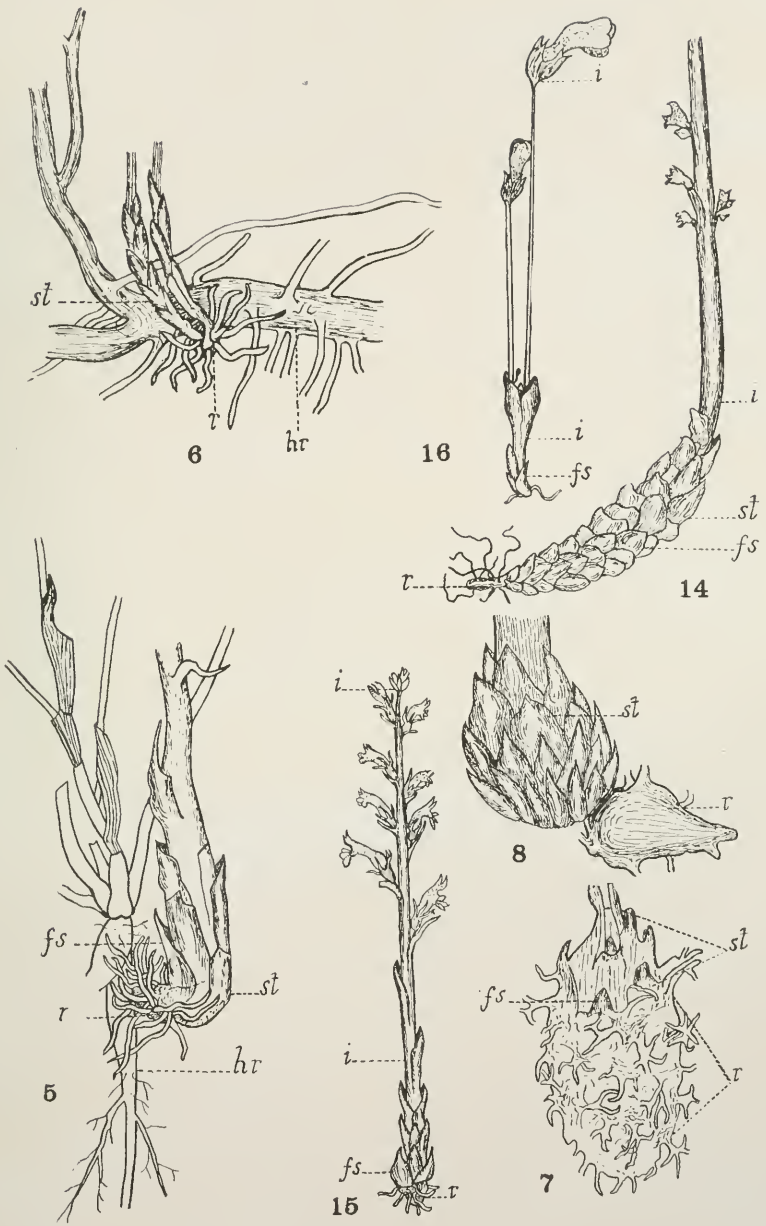
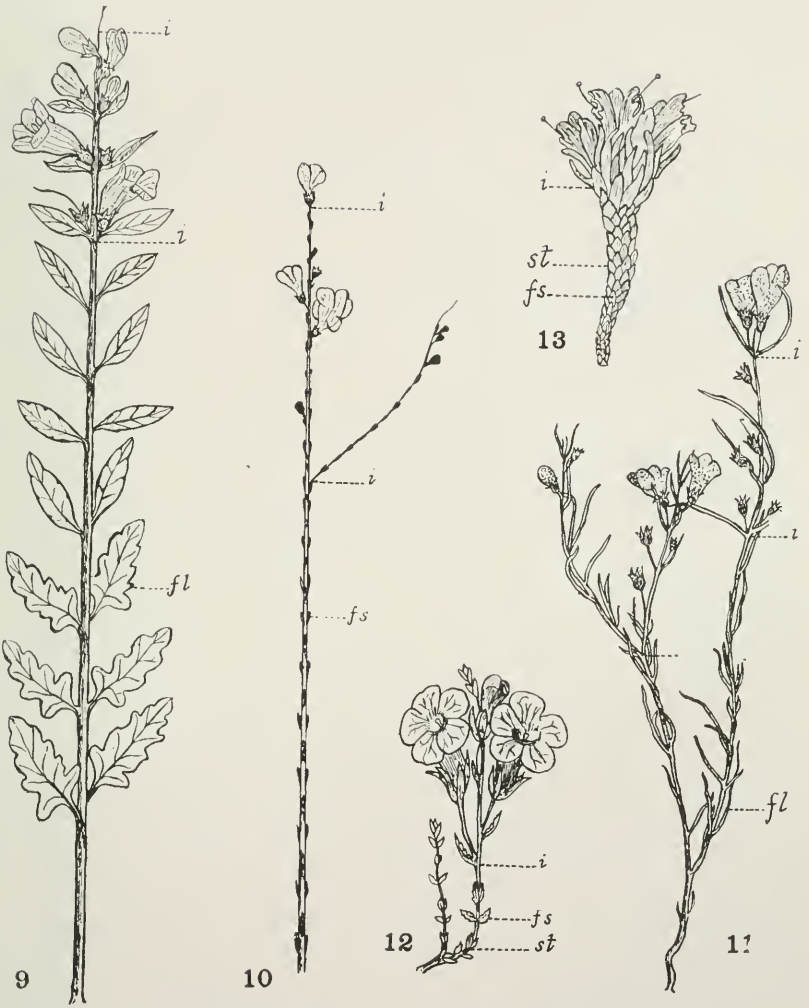
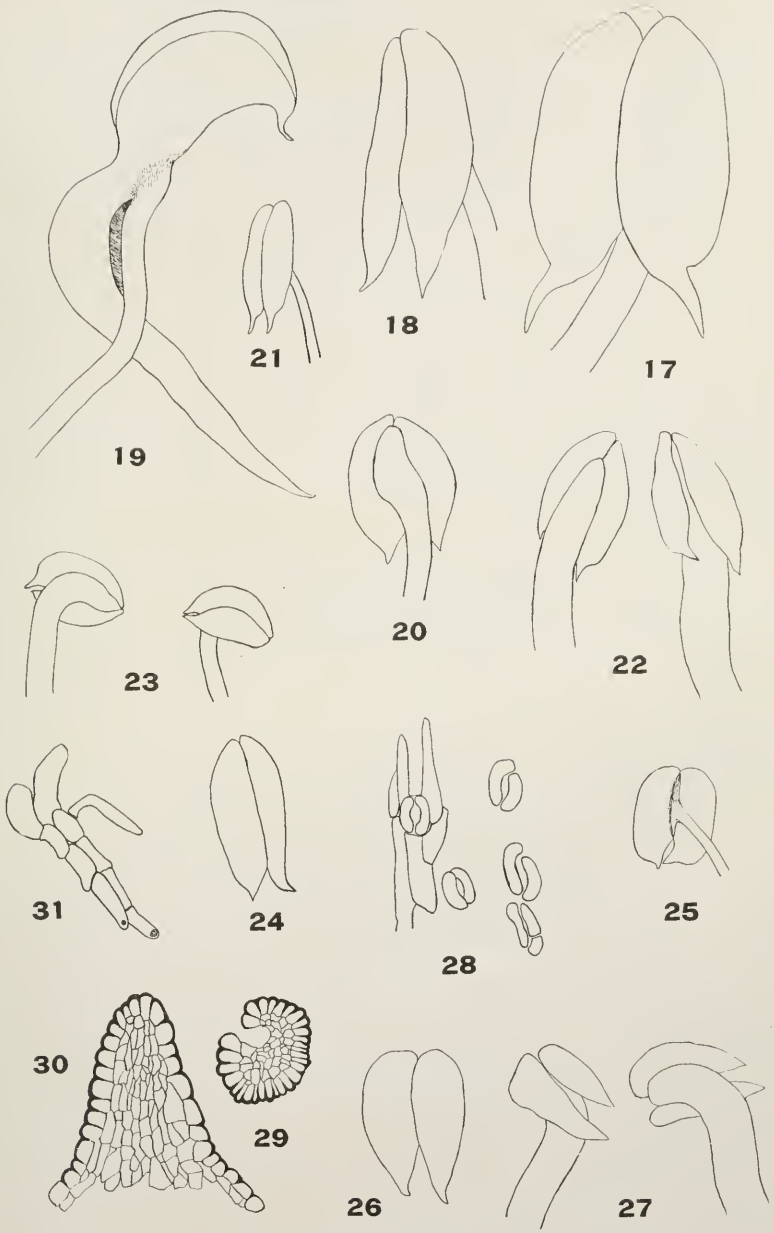
Boeshore on Scrophulariaceae and Orobanchaceae



Boeshore on Scrophulariaceae and Orobanchaceae



Boeshore on Scrophulariaceae and Orobanchaceae



Boeshore on Scrophulariaceae and Orobanchaceae

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Boeshore on Scrophulariaceae and Orobanchaceae

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